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Comparative Psychology

by

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Columbia University

R. H. Waters

University of Arkansas

Calvin P. Stone

Stanford University

F. A. Moss

George Washington University

Donald M. Purdy

University of Kansas

Paul E. Fields

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*Late of the University of California
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Howard S. Liddell

Cornell University

W. T. Heron

University of Minnesota

Edward Chace Tolman

University of California

Robert C. Tryon

University of California

Otto L. Tinklepaugh

Yale University

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Preface

THE increasing number of courses offered in Comparative Psychology gives some indication of the importance of the subject. Realizing the need for a satisfactory textbook in this field, a number of men who had been working in Animal Psychology convened at the Cornell meeting of the American Psychological Association and planned an introductory textbook. Each of them prepared independently a suggestive outline for the book as a whole. After studying this outline, a committee selected what appeared to be the most important topics and allocated the assignments among the men according to their specializations. Thereafter each contributor developed his topic in his own way and assumed full responsibility for content, for interpretation of data, and for placement of emphasis. The book is thoroughly documented, so that anyone wishing to go back to the original sources will have no difficulty in so doing.

The editor wishes to commend the contributors for their systematic team work in attempting to reduce or eliminate needless repetition of closely related subject matter. Perhaps still more along this line, as well as along the line of unification, could have been done had not the time and transport factors rendered personal consultations among the contributors impossible. There was no effort whatever to curb or to eliminate diverse opinions on controversial subjects; such opinions are omnipresent in rapidly changing subjects, and no student is any the worse for encountering them in his reading at the very outset.

Through coöperative efforts, singularly free from the secretive reserve sometimes found among specialists, a book

more representative of Comparative Psychology as it is today has been obtained than could reasonably be expected from the hand of a single contributor in this varied and ever-expanding field. Breadth of view and wealth of subject matter more than compensate for a certain lack of unification inevitably present in a work of this kind.

Washington, D. C.
May, 1934.

F. A. Moss
Editor

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CHAPTER I

Why Study Animal Psychology?

EDWARD L. THORNDIKE

Columbia University

WE may study animals' minds because of scientific curiosity to know what they are and how they work. We may study them because we wish to avoid trouble and to gain efficiency in trapping or killing wild animals or in breeding and raising wild or domestic animals or in using animals as pets or workers. We may study them in order to understand the minds of human beings better or to manage human beings better. For whatever reason we study them, the knowledge and insight gained are likely to increase and refine our knowledge of human nature and our control over it. Man is a vertebrate, a mammal, and a primate, as well as *homo sapiens*. Better knowledge of the behavior of even the lower vertebrates such as fishes and amphibians may lead to better knowledge of the behavior of man. Better knowledge of the behavior of our nearest relatives, the primates, is more likely to do so.

A human mind is the product of original unlearned tendencies and the experiences of life. The former, man possesses as parts of his human inheritance, just as he possesses a backbone, erect stature, small fore-limbs, and a large brain. The latter act upon his mind to change it in accordance with the laws of human modifiability. The original tendencies of man are better known with the aid of knowledge of the original tendencies of our animal rela-

tives; and the laws of human modifiability are better understood through understanding animal learning.

The early psychologists tended to describe each of man's original tendencies or instincts merely as an ability to attain such and such a state or as a proclivity toward such and such a condition. So we were told about the instinct of self-preservation, or the mating instinct. The study of animal instincts encourages, or even requires, us to do more than name the fact that certain states and conditions are more or less attained or favored. For example, the "constructive instinct" so obviously consists of different sets of responses to different sets of conditions in bees, birds, beavers and chimpanzees that we must ask concerning the "constructive instinct" in man, "Just what responses occur, to what external situations, and with the coöperation of what internal circumstances, contexts, or sets of mind?"

The separation of what is instinctive or unlearned from what is added by experience is often easier to make in animals than in man. Thus, a rat's sex-activity may easily be kept free, from birth to adulthood, from all other forces save its inner development and such stimuli as the observer chooses; but no human child's probably ever has been, nor could it be, save at great cost. Indeed, the instinctive tendencies that lead to mating and the influence of experience upon them are perhaps better known in the case of the white rat than in the case of man, in spite of the fact that the former have been the subject of observation by only a few persons for a few hundred hours.

The dates of appearance of original tendencies, their general development, and their waning are conveniently studied in animals. The fighting of chickens can be observed from its first beginnings, where two chicks a few days old confront one another for a second or so and then go about their other business, to the full-fledged cockfight.

Naturalists used to think of an instinct as a power producing a certain response to a certain situation more or less

inevitably and uniformly. Partly as a result of animal experimentation, any such tendency is now thought of as increasing the probability of the response in question, but not necessarily or always to 1.00. Fear of the dark may mean, not that the creature is always or usually afraid when confronted by darkness, but that he is then more likely to be afraid. Darkness plus loneliness may give higher probabilities of fear than either alone. In general, behavior at any moment is a consequence of all the tendencies and fragments of tendencies acting at that moment.

With animals, the development of tendencies can be studied long before birth, by keeping the embryo alive in a medium comparable to that provided by its mother, and subjecting it to various situations. This has been done by Carmichael and his pupils with most interesting results.

The general and fundamental facts of human modifiability are often complicated by the enormous number of modifications that are already made. If you study your learning of French, you need to make allowance for what you know of English and other languages. If you study your likes or your dislikes for new foods, books, or music, you need to measure forces produced by what you have eaten, read, or heard in the past and by the behavior of others toward your past acts and toward foods, books, or music, and to some extent by whatever else happened along with your past experiences. Much of this work is avoided when we study animals. Indeed, it would be possible to observe almost the entire life of an animal so as to have the data whereby to explain nearly all its past and predict nearly all its future.

A generation ago the study of the human mind had described powers and processes such as abstraction, generalization, judgment, reasoning, choice, desire, motives, purposes, attention, the association of ideas, fusion, habit, and automatization; but it had made little progress in working out the dynamics by which these functions operate to make

men think and act and learn. Since then, experiments with human subjects have led to simpler and more fruitful accounts of the causation of human behavior, but the simplest and perhaps the most fruitful have come from the study of animal learning. The formation of mental connections by varied reaction and the strengthening of one of the variants (the so-called animal learning by "trial and error" or "trial and success") has been found at the base of much of human learning. So also has the process of associative shifting whereby a response first connected with a total, say *ABCDE*, is later aroused by *BCDE*, or *CDE*, or *DE*, or *E* alone. It is not important to decide whether more gain has come from using simple general principles found in animal learning to explain the complex and subtle forms of human learning than from studying the latter alone. The former has surely been useful.

Besides providing general principles that may be adequate to account for much, or even all, of human learning, experiments with animals enable psychologists to test hypotheses of all sorts so far as these hypotheses do not involve the action of ideas and impulses that are limited to man. For example, students of general and educational psychology found reason to believe that the same total amount of practice was more beneficial when distributed in decreasing amounts with increasing intervals of time between the doses, than when taken in a few large equal doses near together. Tests of this and other ways of distributing practice with animals have been made with much profit. To obtain facts concerning the relative ability of man to learn at various ages from the same individuals at different ages has been impracticable, and it has been hard to keep such facts free from selective influences when different individuals were used. Check experiments were made upon rats at much less cost of time and labor. Certain experiments with human subjects suggested to the writer that attaching a reward to a mental connection invariably

strengthened it but that attaching a punishment to a mental connection did not in and of itself weaken the connection, but did so only when and as it caused the person to form some alternative connection. He then tested this hypothesis in two ways, first by making a wide variety of experiments with human and animal subjects, and second by analyzing the experiments in which punishment had been attached to connections. The great majority of these experiments had been with animals.

Dr. L. S. Hollingworth has suggested that theories of the causation of neuroses, hysteria, and perhaps certain forms of insanity should be tested by experiments with animals. It surely would be prudent to test such doctrines as that neuroses, hysterias, and the like are due to sex perversions or restraints or psychic shocks by setting up these alleged causes in animals and observing the results in comparison with those in a controlled group. Animals perhaps do not have sufficiently complicated minds to become insane in the ways known among men, but it might be well worth while to apply to them the causes that have been alleged to produce insanities in man. According to a doctrine now popular with psychiatrists and some psychologists, the fundamentals of character and temperament and adjustability to the world are due to the experiences of infancy. Evidence to prove or disprove this theory is very scanty, because in man it is difficult to find good experiences with bad heredity and exceedingly difficult to find bad experiences with good heredity. With certain animals we can provide foster parents of any sort within the range of variation of the species or even robot parents outdoing nature's worst.

A number of problems in the social sciences require for solution knowledge of the relative variability of males and females in the human species. It appears to be a fact that by original nature the ablest and the least able, the best and the worst, the sanest and the most insane are predominantly males. But the truth of this conclusion has been disputed

and probably will be until, by nature or by artifice, males and females are somewhere given equivalent training. A fair comparison can, however, be made at any time with the males and females of many other species of mammals.

The problems concerning mental inheritance in man are made difficult by the small number of children of the same parents, and by the fact that inheritance is confused and distorted by family training. Most of these problems should be worked out first in the lower animals, among which we can easily collect a score of brothers and sisters for study, and the training of which can be controlled by the experimenter.

The study of animals not only supplements human psychology and helps to solve problems arising therein: it also suggests new problems and new methods for human psychology. If one were to choose the half dozen discoveries of recent years that have most influenced human psychology, Pavlov's discovery that the act in dogs of secreting saliva could be attached to any stimulus would surely be included. The most hopeful methods of measuring motives and of balancing one desire or motive against another were developed by Moss, Warden, and others in the study of the relative strength in the white rat of hunger, sex desire, and the desire of the mother to reach and attend to her young.

Certain important aspects of human nature such as are covered by the psychology of language, music, science, and business have received enlightenment from the study of animals only indirectly, through better knowledge of general principles. The special sense-powers and motor skills and organizations of ideas of man also are usually best studied directly in him. Not everything in man is enough better understood by knowing its development in the animal kingdom to justify its study in the animals, and the development in the animal kingdom of some traits of the human mind probably never can be known. Man's ancestors parted

company with the ancestors of the chimpanzees and gorillas millions of years ago. How we came to devise language and mathematics and be psychologists while the great apes became our prey or pets, the apes certainly cannot be expected to tell us. However, about fundamental problems in original tendencies and learning, they and the mammals in general have much to tell us; and the student of these aspects of human nature will profit greatly from knowledge of animal psychology.

The special student of human mental evolution should also know all the relevant facts about our nearest living relatives as fast as these facts are discovered. Some of their traits, such as their curiosity, manipulative skill, and love of experience for experience's sake, justify the leading investigator of primate psychology in entitling a book about them *Almost Human*. Some of the traits by which they and man are distinguished from other mammals are less estimable, such as sex indulgence in season and out of season. It is fairly probable that inspecting a comrade's skin for small loose particles living or dead and disposing of the same by eating them is another ancient bond of union.* The latter feature should not unduly lower the reader's opinion of his far-off ancestry. Mutual aid may have had its roots in such lowly forms as well as in the more esteemed mother love and group protection. Science must follow the facts wherever they lead.

* See R. M. Yerkes, "Genetic Aspects of Grooming, a Socially Important Primate Behavior Pattern," in the *Journal of Social Psychology*, 1933, Vol. 4, pp. 3-25. He summarizes the essential features of a behavior widespread among primitive men as follows: "The hair of a companion, irrespective of sex, is examined visually and with the aid of the fingers, for parasites and other foreign objects. When a parasite is found it usually is picked up and either popped with the finger nails, and thereupon carried to the mouth and swallowed, or instead crushed by the teeth before swallowing."

CHAPTER II

The Historical Background of Comparative Psychology

R. H. WATERS

University of Arkansas

COMPARATIVE psychology is a relatively dull and prosaic affair until the time of Darwin in the nineteenth century. Then a new spirit was injected into the subject; studies of animal behavior took on a greater significance as a means of explaining human behavior; and the field won comparative freedom from its philosophical parent. The result is that now one finds himself almost enthusiastic over the more recent advances in the field and faces the future with a stimulated faith in man's ability to explore its problems adequately.

If all the things we know do not have an ending, they at least have had a beginning, and prototypes of contemporary views and theories can be found in preceding decades. Thus, for the sake of a historical sophistication, which is supposed to make one more appreciative of current hypotheses, it is worth while to learn how men of periods preceding ours have thought, studied, and theorized about the same problems that cause us concern; how discoveries and hypotheses of each age have provided the basis for the subsequent development of still more penetrating theories and methods; and how the formulation of more helpful suggestions has sometimes been hindered by the concepts and beliefs of an earlier period.

It is difficult to determine when interest in animal behavior began. Archæological discoveries indicate that at least it antedates historical records. The discoveries most important for comparative psychology are the paintings, drawings, and sculptures of animals found in caves inhabited by prehistoric man. These works of art date as far back as from twenty-five thousand to thirty thousand years ago. What significance they possess is problematic. It is thought that they were made in connection with religious ceremonies or formed a part of certain more or less superstitious rituals. For example, some of the sculptures are mutilated and bear the marks of spear thrusts, blows, and so forth, which may indicate that our ancestors were perhaps trying to invoke the aid of the gods in the chase—a sort of forerunner of the more modern practice of burning enemies and public officials in effigy. Whether they had this significance or whether these primitive artists, when the artistic impulse was upon them, turned to nature for their subjects, it is perhaps significant that at that early date man was apparently taking more notice of the animals than of the plants surrounding him.

In ancient Egypt, Greece, and Rome, the behavior of animals and, especially, of birds was thought to be of prophetic significance. The way in which the birds of augury took the grain spread before them and whether they ate it at all were indicative of future events. Similar significance was attached to the behavior of certain animals. The way in which certain reptiles moved or avoided obstacles was important in these rituals. Important undertakings—such as wars, voyages, marriages, induction into public offices, and perhaps even trips to the market places—were undertaken only when the behavior of the birds of augury was favorable. Possibly Cæsar was warned against going to the Senate on the Ides of March on some such basis.

From these small beginnings it is a far cry to the comparative psychology of today. It is the task of a historical

introduction to picture how, in successive ages, man has produced new theories; raised new problems; introduced new methods and experimental techniques; withal, how he has changed the place occupied by comparative psychology in the thought of succeeding periods. Perhaps, also, the student may hope for a better acquaintance with the men who have left their impress on the development of the subject.

To make the survey somewhat lighter, we shall divide the history of the whole movement into five different periods for separate discussion. In connection with each of these periods it may be well for the student to try to understand these three phases: first, the philosophical systems that furnished the background of thought for comparative psychology; second, the methods and techniques that were employed or developed; and third, the types of problems that engaged the attention of the workers. Only the barest framework will be presented—a short chapter can furnish no more. For a fuller treatment of any period a somewhat voluminous literature may be consulted.

The Grecian Period

It was in the Grecian era that for the first time, as far as historical records show, man began to deal in a serious fashion with the problems presented to him by his universe. For the Greeks the chief interest was cosmology, the problem of the structure of this universe. Their treatment of animal behavior, with the possible exception of the studies by Aristotle (384–322 B. C.), was wholly incidental to this major program and formed but one phase of their more general philosophical inquiries into all natural phenomena.

Several theories still alive in comparative psychology found their first expression with the Greeks. Both the dualistic and monistic conceptions of the universe, which are basic to the present vitalistic-mechanistic controversy,

were formulated during this period. The dualistic conception was introduced by Empedocles about 500 B. C. and was modified by Anaxagoras (500–428 B. C.). These philosophers held that material objects were ultimately reducible to physical elements—fire, earth, air, and water. They felt, however, that non-physical principles must be assumed in order to account for the organization and movement of these elements. For Empedocles these non-physical principles were attraction and repulsion or love and hate. Anaxagoras substituted for these two a single principle, Mind. Opposed to this dualism was the monism, a materialistic monism, of Leucippus and Democritus (460–370 B. C.). On this theory the atoms composing matter were endowed with the power of movement. Hence no use was made, for no need of it was felt, of any non-physical principle, soul, mind, or world-ordering Intelligence in accounting for the organization and movement of these atoms. This conception figures prominently in contemporary behavioristic psychology.

Plato (427–347 B. C.) continued the dualistic argument and offered a theory of the soul that made for a clean-cut difference between man and animals. He held for a division of the soul into an irrational part and a rational part. The latter part was peculiar to man alone. The irrational soul was further divided into two parts. The spirited part had its seat in the breast, and the appetitive part was located in the abdomen. These three divisions, for Plato, corresponded to the three levels of organic life—plants, animals, and man.

Even in those good old days a theory of evolution had developed. Empedocles taught that life came from lifeless matter—the doctrine of abiogenesis or, in modern phraseology, spontaneous generation. Plants were supposed to develop from lifeless matter first; and from plants, animals—or rather parts of animals—were developed. These parts, a head without a body, arms with no shoulders, and so on,

were subject to the operation of the two principles, attraction and repulsion, and thus were joined. Any number of grotesque combinations probably resulted. Those combinations not adapted to their environment disappeared because they could not reproduce. Nature tried other means, finally succeeding after several abortive efforts in perfecting types that fitted their surroundings and were capable of reproducing their kind. Thus we have higher forms succeeding lower—an important feature of more modern theories.

Such was the type of speculative approach to the study of animal behavior prior to Aristotle. A somewhat different procedure was introduced by him. Becoming discontented with the prevailing method, he made the first plea for careful investigation, observation, and gathering of facts before formulating theories. He observed these three points to some extent, at least, in his own studies. His writings of major interest for comparative psychology are his *Historia Animalium*, *De Partibus Animalium*, *De Motu Animalium*, *De Incessu Animalium*, and *De Generatione Animalium*, although many of the concepts developed therein are intimately related to certain of his other writings, of which should be mentioned the *De Anima*.

The strictly inductive method that he proposed was an ideal which he approached but never quite reached, since he brought to his studies of animal behavior certain philosophical conceptions that colored his interpretation of all natural phenomena. He assumed a teleological sequence in the universe: "Nature creates nothing without a purpose, but always the best possible in each kind of living creature by reference to its essential constitution." * Also, instead of proceeding empirically on the matter of the origin of animals, he constructed an elaborate theory of an ultimate principle, Reason, which coöperated with several

* Aristotle, *De Incessu Animalium*, Book 2, page 704^b, lines 15-18.

other principles to cause every object to appear in the form it possessed.

Before Aristotle could take up the study of animals, he considered it expedient to give a vigorous defense of such investigations. Animals should be studied, he argued, not only for the sake of better understanding this part of man's environment but also because this field, perhaps even better than astronomy, should help man to detect nature's plan and to decipher the principles in harmony with which this plan was carried out:

In certitude and in completeness our knowledge of terrestrial things has the advantage . . . For if some (animals) have no graces to charm the sense, yet even these, by disclosing to intellectual perception the artistic spirit that designed them, give immense pleasure to all who can trace links of causation, and are inclined to philosophy. . . . If any person thinks the examination of the rest of the animal kingdom an unworthy task, he must hold in like disesteem the study of man. For no one can look at the primordia of the human frame—blood, flesh, bones, vessels, and the like—without much repugnance. Moreover, when any one of the parts or structures, be it which it may, is under discussion, it must not be supposed that it is its material composition to which attention is being directed or which is the object of the discussion, but the relation of such part to the total form.*

These statements, which give at once his defense of the study of animals, have a distinctly modern ring, although at the present time no such defense is needed.

The *Historia Animalium* is essentially a natural history of animals. In it is discussed with considerable detail the differences between animals of different species in certain physical traits; the habits of locomotion, breeding, and mating; nesting habits; care of young by animals and man; puberty in man, and childbearing. Animals are credited with having characters just as are men:

Some are good-tempered, sluggish, and little prone to ferocity, as the ox; others are quick-tempered, ferocious, and unteachable, as the wild

* Aristotle, *De Partibus Animalium*, Book 1, Part 5, page 645^a, lines 1-34.

boar; some are intelligent and timid, as the stag and the hare; others are mean and treacherous, as the snake; . . . some are crafty and mischievous, as the fox; some are spirited and affectionate and fawning, as the dog; others are easy-tempered and easily domesticated, as the elephant; others are cautious and watchful, as the goose; others are jealous and self-conceited, as the peacock.*

The mass of material contained in these writings, when viewed against the background of earlier Greek thought, is staggering. The range of subject matter in itself is colossal. (Aristotle is said to have distinguished and described no less than five hundred different species of animals in his works.) There are, of course, according to modern standards, some obvious defects in his work. It is difficult to determine how much of his factual material was due to his own personal observation; how much was done by others under his direction; and how much was borrowed from other writers. There is a disconcerting mixture of really fine observational work and of fanciful anecdotal material. As examples of the first we have his careful study of the development of the embryo of the chick and his study of the habits of the bee and of certain fish. As examples of anecdotes these are illustrative: "Dogs show their dreaming by barking in their sleep"; † "In the neighbourhood of Lake Mæotis, it is said, wolves act in concert with the fishermen, and if the fishermen decline to share with them, they tear their nets in pieces as they lie drying on the shore of the lake"; ‡ and, with reference to the breeding of sheep, " . . . when north winds are blowing, they are apt to bear males; if when south winds are blowing, females."# (A zoölogist colleague of the author, who is also a wag, has asked what would happen in a calm or a cy-

* Aristotle, *Historia Animalium*, Book 1, Part 1, page 488^b, lines 12-24.

† *Ibid.*, Book 4, Part 9, page 536^b, line 51.

‡ *Ibid.*, Book 9, Part 36, page 620^b, lines 6-9.

Ibid., Book 6, Part 19, page 573^b, lines 38-39.

clone.) Such a mixture of truth and fancy makes it difficult to separate the grain from the chaff. Further, too little information of any one genus or species is given to offer more than a point of departure for more refined work.

Aristotle's physiological conceptions are amusing when compared with our present knowledge. He argued that the heart was the seat of all the higher psychical processes, because it was the first organ to be seen manifesting life in the developing embryo (based on his own observations of the chick), and because whatever was the most important would be found in the center, just as the earth was the center of the universe. Secondly, he held that the brain was not connected with any sense department or psychical function. This, he argued, was true because observation revealed it and also because no sensation was produced when it was touched (an observation now known to be correct). The function of the brain was that of a cooling mechanism for the heart—a type of refrigerating apparatus—and tears were considered the result of the cooling action of the brain, which had caused a condensation of the vapors of the blood. It was for the sake of keeping the brain cool that the head had no flesh on it, and thus permitted the readier radiation of the heat from that organ. As our zoölogist friend has remarked, the general morphological scheme seems to have been that of the General Electric refrigerator! Aristotle also taught that the brain, of all the fluid (*sic!*) organs of the body, was the driest, being most free from blood.

Of the formulations that are of most importance for comparative psychology, we find the following. He distinguished three souls that were present in the animal kingdom: the nutritive soul, which ruled over nutrition and reproduction in all animals and plants; the sensitive soul, not found in plants, arbiter of sensations and, in some of the higher animals, of locomotion as well; and the rational soul, peculiar to man. A few special doctrines are interesting as

illustrative of his thought: "Many animals have memory, and are capable of instruction; but no other creature except man can recall the past at will";*

In the great majority of animals there are traces of psychical qualities or attitudes, which qualities are more markedly differentiated in the case of human beings. For, just as we pointed out resemblances in the physical organs, so in a number of animals we observe gentleness or fierceness, mildness or cross temper, courage or timidity, fear or confidence, high spirit or low cunning, and, with regard to intelligence, something equivalent to sagacity. . . . The truth of this statement will be the more clearly apprehended if we have regard to the phenomena of childhood: for in children may be observed the traces and seeds of what will one day be settled psychological habits, though psychologically a child hardly differs for the time being from an animal.† [Aristotle, apparently, had no higher opinion of the child than do maiden ladies today.]

We also find a forerunner of the much maligned "Law of Effect" in that "whatsoever is in conformity with nature is pleasant, and all animals pursue pleasure in keeping with their nature."‡ Aristotle's doctrine of evolution differed from earlier ones. He argued that the animals formed one continuous series from lower to higher, but that the higher did not evolve from the lower. Rather, all organisms were subjected to an "internal perfecting principle" that constantly strove for a perfect type. Or, as it has been said, evolution worked from above downward rather than from below upward.

The following points serve to indicate the heritage that succeeding periods owe to Aristotle. First, he had developed the concept of teleology, which finds its adherents today among psychologists and philosophers; second, he sponsored the concept of vitalism—the doctrine that a strictly mechanical explanation cannot account for the com-

* *Ibid.*, Book 1, Part 2, page 488^b, lines 25-27.

† *Ibid.*, Book 8, Part 1, page 588^a, lines 18-36. .

‡ *Ibid.*, Book 8, Part 2, page 589^a, lines 8-10.

plexities of animal behavior; third, he left a wealth of data for other workers to ponder over—to accept or reject as their own researches give them license; fourth, he was the champion of observation as the primary and only safe method in natural science; fifth, more distinctly important biologically, he left a classification of the animal phyla that was accepted as standard until that of Linnæus made in 1735; sixth, he had developed a doctrine of evolution and by so doing kept that problem alive, although his doctrine differed from that of modern times. Thus, in spite of the defects in his work, in spite of his reliance upon the unsound anecdotal method, Aristotle heads the list of important figures in the history of comparative psychology. Perhaps no greater tribute has been paid him than that by Darwin, who wrote that, in comparison with “Old Aristotle,” Cuvier and Linnæus were “mere schoolboys”!

The development of thought during the Grecian period reached its peak in Aristotle. Little of importance was contributed by the men who followed him. The Stoic and Epicurean philosophies deserted the dualistic position attained by Aristotle and returned to the fold of Democritus. The Stoics are credited by Wilm with the development of the concept of instinct. They clothed it in a dress that carried the modern lines. Anecdotal material was contributed by Pliny (23–79 A. D.), Plutarch (c. 46–120), and Porphyry (c. 233–304). Although such material has little value, we should not be too hard on these men. Even as late as the critical nineteenth century such material was soberly proposed as evidencing the intellectual achievements of the brute. Truly let him who has not sinned cast the first stone!

The picture of animal study left us by the Greeks may be briefly outlined as follows. Their interest in the animal was dictated by their more general inquiry into the nature of the universe as a whole. They were primarily interested in accounting for the origin and development of animal

forms rather than in a detailed study of their behavior, although Aristotle forms a notable exception to the general run of thinkers of that age. The methods characteristic of this period were of the speculative, philosophical variety eked out by anecdotal materials. Here again Aristotle cannot be forced into the picture, for in some of his own studies he employed the handmaiden of contemporary science—objective observation. The type of problems investigated dealt largely with the behavior of the animal as it took place in his natural environment. Strictly experimental studies as we think of them today were not in vogue. The maze and the problem box had not been invented!

The Middle Ages

One of the most barren periods in our history was the period known as the Middle Ages. Then the Church assumed a dictatorship over what man should believe and what man should investigate. In so doing the Church Fathers claimed not only the authority of the Bible but, strange as it may seem, the authority of Aristotle as well. This latter authority the Church owed to the influence of Augustine (354–430), Thomas Aquinas (1225?–1274?), and Albertus Magnus (c. 1206?–1280). These men combined Biblical teachings with those of Aristotle to give a naturalistic account of nature and life. So successful were they in this attempt that the Church and the Scholastic thinkers frowned upon original investigation and refused to accept any statement of fact unless it was contained in Aristotle. The story is told that a budding young investigator claimed to have seen the spots on the sun through a telescope. One of the Scholastics is reported to have said to him that a diligent search of Aristotle revealed no mention of any such spots and that therefore the investigator should be assured that the spots were in his eye or in his telescope and not in the sun! Such an attitude meant a decline in

scientific interest and research along all lines. The period was thus marked by a scientific sterility unparalleled in history. Only in Arabia and through Arabian workers was interest in science kept alive. Their interest centered chiefly in medicine and physiology. From their work an indirect benefit resulted for comparative psychology in that they held that natural laws controlled physiological mechanisms, and the fact that they did so quite possibly served to stimulate others later to champion similar laws for more complex forms of behavior.

The Renaissance

The return of scientific investigation of natural phenomena during and following the Renaissance was due as much to the influence of philosophers as to that of scientists. During this period Francis Bacon (1561–1626) openly decried the natural science of the Greeks, championed the inductive method in science, and urged particularly the study of the species and varieties of animals for the purpose of arriving at a logical explanation of their origin and relations.

Similar arguments were advanced by René Descartes (1596–1650), who is important for two reasons. He argued for the right to investigate natural phenomena unhampered by the Church and offered some general principles for explanation of the nature of the universe. Secondly, he developed the notion that animals were automata, and hinted that perhaps man was not the wholly rational animal he was thought to be! Perhaps this suggestion was anticipated or made possible by the earlier work in physiology, especially that of Harvey, who had demonstrated the circulation of the blood. These earlier workers had shown that the living processes of the organism were the result of certain chemical and physical laws.

Descartes applied the same sort of hypothesis to the actions of the individual.

However, Descartes, though bold, did not dare flaunt the authority of the Church too much. He pointed out that it might be entirely possible to reach an intelligible solution of the order of the universe on the basis of some rational hypotheses. He hastily added that of course everyone knew that the universe did not actually develop according to such principles. Thus he escaped the Inquisition! Further, he did not deny the existence or importance of the soul in the behavior of man. The soul had its seat in the pineal gland, the only gland that has direct connection with both hemispheres of the brain and that hence might enable the soul to be in direct communication with both. Here the soul resided and directed the flow of animal spirits. Descartes thus kept alive, be it noted, the tradition of a qualitative difference in the behavior and nature of man and animal. So far as is known, he never made any particular use of the soul after he had safely ensconced it in the gland. He proceeded to account for behavior in terms of physical principles, but since he had the soul in his system of beliefs, he escaped the more serious criticism of the Church.

Leibnitz (1646-1716), Spinoza (1632-1677), Hume (1711-1776), and Kant (1724-1804) joined in the chorus for a naturalistic interpretation of nature as opposed to the interpretation sponsored by the Church. Kant, though he argued for the desirability of such a naturalistic interpretation, was rather of the opinion that such an attempt did not lie within the power of man. Because the theory of evolution had such a tremendous influence for animal study later, Kant's view of the possibility of some such theory is interesting. Man, he held, was simply not capable of envisaging principles of sufficient generality to account for the development of the various animal forms. It was "absurd

for man . . . to hope that a Newton may one day arise even to make the production of a blade of grass comprehensible, according to natural laws ordained by no intention." * However, as Osborn points out, Darwin was Kant's Newton who did just that thing!

Thus through philosophical efforts the way was being cleared for a return of the scientific investigation of animal behavior. Other contributory forces leading to the same end were also developing. Aided by the new microscopic techniques, studies in physiology were revealing more and more of the *modus operandi* of neurophysiological mechanisms. A more adequate classification of animal forms had been proposed by Linnæus. The works of Buffon (1707–1788) in natural history and of Bonnet (1720–1793) on insect forms, to mention but two of a considerable number of important men, were stimulating the interest of scientific men to more refined studies. It was practically inevitable that man's interest would reach out to include studies of animal behavior. But the most potent force toward animal study was still to come—the influence of the theory of evolution. As will be shown later, the nature of the theory was such that it inevitably led beyond the zoölogical to the psychological study of animal life.

The Middle Ages formed a "strange interlude" during which theology had the whip-hand and made scientific investigation a disgrace. This interlude was passing during the Renaissance. Beneath the surface, rumblings of a coming storm were heard. Men dared to oppose theology—dared to champion man's right to an impartial study of nature's phenomena. Throughout this period, as remarkable for the manifestation of this spirit as was the Middle Ages for the lack of it, there was the promise of a return to a belief in natural laws.

* H. F. Osborn, *From the Greeks to Darwin*, page 100.

The Darwinian Period

So tremendously was comparative psychology influenced by Charles Darwin (1809–1882) and his theory of descent in the period following the Renaissance that this period is properly designated as the Darwinian Period. Charles Darwin grew up in an atmosphere that was charged with the general problem of the development of the species. Lamarck's theory, presented in 1802, was being debated by Cuvier and St. Hilaire, two prominent biologists of the time; studies in embryology were showing the startling similarity in the embryonic forms of different species; naturalists in France and Germany were contributing to the theory—in a word, a “storehouse of facts was fairly bursting for want of a generalization” * when Darwin appeared on the scene. Darwin's grandfather, Erasmus Darwin (1731–1802), had been interested in the problem and had written his *Zoönomia* in 1794. This important work presented a theory similar to Lamarck's. One is tempted to think that perhaps Lamarck borrowed from Erasmus Darwin, but Osborn believes it probable that both men reached the same theory independently.

Darwin's first interests were geology and natural history. In part because of these interests, he obtained the post of naturalist aboard the ship *Beagle* for a round-the-world cruise during 1831–1836. It was probably the observations and questions raised during this voyage that finally led him to undertake the formulation of his theory, embodying the well-known principles of Variation, Struggle for Existence, and Selection, or the Survival of the Fittest. His complete statement appeared in his *Origin of the Species* (1859). More important for the study of animal behavior, however, are two other books, *Descent of Man* (1871) and *Expressions of the Emotions in Man and Animals* (1872).

* *Ibid.*, page 231.

These two books represent essentially Darwin's attempt to apply the general principles developed in the *Origin of the Species* to the physical, mental, and emotional development of man. In the *Descent of Man* he first stated and defended the case for the physical development of man from some preëxisting form and then turned to the more important and difficult task of explaining mental development. He argued that since there is really less difference between the higher apes and man than there is between the higher apes and the lowest fishes, and that since likewise within the human species there is no break between the least and the most intellectual, therefore from the lowest animal to the highest man there is a quantitative, but no qualitative, difference, and consequently the two are connected by a series of fine gradations. In support of this thesis he adduced the following facts: Both possess similar senses, similar instinctive action, the same fundamental emotions, and the higher mental processes of attention, memory, imagination, deliberation, and choice. He even argued that animals show a trace of what, if the animal's intelligence equalled that of man, would be language, a sense of beauty, a moral sense, and a belief in spirits! By far the most of the evidence he cited in support of these claims was of the type we now call anecdotal in nature. No precise experimental investigations were made to obtain crucial data—the world had not yet heard of Lloyd Morgan! One instance of such material may be given:

Sir Andrew Smith, a zoölogist whose scrupulous accuracy was known to many persons, told me the following story of which he was himself an eye-witness: At the Cape of Good Hope an officer had often plagued a certain baboon, and the animal, seeing him approaching one Sunday for parade, poured water into a hole and hastily made some thick mud, which he skillfully dashed over the officer as he passed by, to the amusement of many bystanders. For long afterward the baboon rejoiced and triumphed whenever he saw his victim.*

* Charles Darwin, *The Descent of Man*, page 85.

In the *Expressions of the Emotions in Man and Animals* Darwin traced man's emotional development from lower forms. Some of the evidence presented would not be considered convincing according to modern standards. True, he made some observations of his own on infants and common animals, but much of his material was drawn from the reports of others who made observations at his request. The latter reports, however, seem to be largely anecdotal in character and hence are of questionable value. Paintings and sculptures furnished a third source of materials used by Darwin to advance his thesis, but these, he admitted, were not particularly useful.

Although the evidence given by Darwin does not measure up to modern standards of scientific exactness, the claims he made naturally stimulated many workers to devise experimental situations to test his hypotheses. In addition he influenced the development of comparative psychology through the emphasis that he placed upon the genetic method. It was felt by some who followed Darwin that an adequate account of any type of behavior should be based on its phylogenetic and genetic history. To a greater extent his work influenced psychology in general through providing the basis for the functional school of psychology. Darwin stressed "mind" as so important in making for adaptation that thereafter more and more psychologists came to consider mind as an instrument whose *functions* were to be studied rather than as a series of static states whose contents were to be analyzed. These three influences are still vital forces in contemporary psychology. The one thing, however, that was most characteristic of the period immediately following Darwin was probably the vigorous search for and claims of higher mental traits in animals. It was here that the chief problem lay for those who would accept Darwin's theories. Little objection was made when man was said to have lower traits in common with the animals, but to say that man and animals alike

possessed higher mental processes was to raise the brute to the level of man, or to lower man to the level of the brute, and this struck fire. Accordingly it behooved investigators to establish the fact of these higher processes in animals.

The most important of the immediate followers of Darwin was G. J. Romanes (1848–1894). His works, *Animal Intelligence* (1882), *Mental Evolution in Animals* (1883), and *Mental Evolution in Man* (1888), form a triad bearing particularly on the evolutionary doctrine applied to mental traits. So important were these writings in the field that Boring describes him as being Darwin's apostle in comparative psychology. Romanes continued the plan outlined by Darwin and argued for the continuity of animal and human mind. Since he made liberal use of anecdotal material, his contribution to animal study lacks really good support. A typical instance may be given:

Watch is a collie dog . . . a very remarkable dog . . . very intelligent, understands many words, and can perform tricks. What I mention him for, however, is that he is the only dog I ever met with a dramatic faculty. His favourite drama is chasing imaginary pigs. He used now and then to be sent to chase real pigs out of a field, and after a time it became a custom . . . to open the door for him after dinner in the evening, and say, "Pigs!" when he always ran about wildly chasing imaginary pigs. If no one opened the door, he went to it himself wagging his tail, asking for his customary drama. He now reaches a further stage, for as soon as we get up after our last meal he begins to bark violently, and if the door is open he rushes out to chase imaginary pigs with no one saying the word "pigs" at all. He usually used to be sent out to chase pigs after prayers in the evening and when he came to my small house it was amusing to see that he recognized the function of prayers performed with totally different accompaniments to be the same as prayers performed in an episcopal chapel, so far as he expected "Pigs" to be the end of both. The word "pigs," uttered in any tone, will always set him off playing the same drama.*

This particular case was given, Romanes says, to show

* G. J. Romanes, *Mental Evolution in Man*, page 56.

"imaginative faculty in animals" and because it "appears to show that this kind of imaginative play may extend in animals, as in children, to the still higher level not only of pretending that inanimate objects are alive, but of 'peopling space with fancy's airy forms.' " *

The dangers of the anecdotal method, which today is rarely used, were made so apparent by Romanes's use and abuse of it that after the publication of his works this method was seriously discredited. Consequently a pertinent question to ask is, What is the method and what is wrong with it. This answer may be given: The anecdotal method is being employed whenever an individual's report of some item of animal behavior is accepted as valid if the controls surrounding the observation and report do not measure up to modern scientific standards. The lack of such controls allows the following errors to vitiate the report: the individual does not distinguish between what he observed and what he read into the act; the individual does not know the habits and the past training of the animal observed nor those of the species to which it belongs and he therefore reports an incident lifted out of its proper context, which would give the act a truer meaning; lastly, his interpretation is biased by what he believes concerning animal intelligence in general and the intelligence of that animal in particular.

Significant Movements Since Darwin

The anthropomorphizing tendencies thus initiated by Darwin and carried to the extreme by Romanes received some pretty definite checks at the hands of other writers. Some checks comparative psychology could well ignore as being dogmatic, emotional outbursts only. On the other hand, some were the reasoned and serious opinions of scientifically trained men and had to be taken into account.

* *Ibid.*

The most important example of the latter was the opinions of C. Lloyd Morgan (1852–). His writing that was perhaps most important for comparative psychology, at least from the standpoint of methodology, was his *Introduction to Comparative Psychology* (1894). He recognized that the interpretation of the animal mind rested on the analogy with that of man; that the interpretation was liable to error in that too much mind might be ascribed to the animal; and that some guiding principle was needed to avoid this mistake. He therefore proposed what has since been known as "Lloyd Morgan's Canon," a form of the law of parsimony. This canon was formulated as follows: "*In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale.*"* Morgan tried religiously to live up to this principle and it has since continued to influence the type of explanation offered by investigators—so much so that "the term 'anthropomorphic' acquired a peculiar significance in certain quarters. It became a choice epithet which you could hurl at an antagonist with telling effect when you wished to damn him in genteel terms. The word as used in this way seemed to convey the somewhat delicate suggestion that the individual in question was obtuse in intellect, a logical pervert, and an insipid sentimentalist."† Gestalt psychologists have taken up cudgels against the canon, arguing that in psychology there is need, and in comparative psychology still greater need, for qualitative descriptions, which are not allowed on the basis of the canon. Gestalt psychologists may be right. Our guiding principles must be sufficiently broad and elastic to act as guides only and not as masters.

In the *Introduction to Animal Life and Intelligence*

* C. L. Morgan, *An Introduction to Comparative Psychology*, page 53.

† H. A. Carr, "The Interpretation of the Animal Mind," *Psychological Review*, 1927, Vol. 34, page 88.

(1891) (rewritten as *Animal Behavior* in 1900), as well as in his other writings, Morgan reported considerable experimental data drawn from his own observations. These observations, though experimental, were field studies rather than laboratory studies, and may be classified with such studies as those of Fabre on wasps and bees, those of the Peckhams on the solitary wasps, those of Lubbock on ants, wasps, and bees, and those of others.

Another important figure who argued against the anthropomorphic tendency was Jacques Loeb (1859–1924), whose relevant work began to appear in 1890. He developed what is known as the tropism theory. On this theory animal behavior can be explained satisfactorily in terms of physicochemical principles of exactly the same nature as those that explain the orientation of plants to outside forces. He refused to use the term “trial and error” or to employ terms suggestive of mental processes. Loeb’s ambition was to explain animal behavior not from the standpoint of the introspective psychologist but from that of the physical chemist. Any other type of explanation, he argued, was bound to end in failure, if for no other reason than that it would not lead to quantitative experiments. Animals were automata and, like lifeless matter, were the puppets of external forces. Most of Loeb’s work was done on lower animal forms, but he clearly implied throughout his discussions that he believed the same explanatory principles could be applied safely to the behavior of higher forms and of man as well. He did admit of “associative memory” in higher forms, but this term was a poor symbol for the changes left on neural structures by previous action. In Loeb, then, we see something of a return to Descartes and the earlier Grecian materialists, Democritus and Leucippus, and a continuation of the mechanistic argument.

In opposition to the tropism theory is the “trial and error” doctrine defended by H. S. Jennings (1868–). On the basis of some really remarkable work on lower pro-

tozoan forms during the close of the nineteenth and the opening of the twentieth century, he was able to show that animals of even these low orders do not behave in a manner harmonious with the tropism theory. His experiments showed that when these animals orient themselves to various stimuli that, according to Loeb, bring out tropisms, several preliminary movements or "attempts" occur before their response, in its final form, takes place. This being so, Jennings argued that the term "trial and error" was a better descriptive phrase to apply to the behavior than "tropism."

During the close of the nineteenth and the opening of the twentieth century, a distinctly different phase of the movement in comparative psychology appeared. For the first time definitely experimental and laboratory studies made their appearance. Interest shifted from the attempt to determine the similarities in the behavior of man and animals to that of determining precisely what, under controlled conditions, animals can do. America became the theater of the movement. New methods and techniques particularly adapted to the study of animals were developed and applied. In a word, the definitely experimental stage of the study arrived. With these changes there inevitably has appeared a broader range of problems, which present such a bewildering complexity that an adequate summary of all of them cannot be given. The remaining chapters will give an indication of the wealth of material being accumulated. Here it is necessary only to indicate some of the more distinctive and important trends.

The present stage of comparative psychology may be said to have been initiated by the genius of Thorndike (1874-), who, in 1898, began to publish his studies on the learning behavior of cats, dogs, chicks, and monkeys. His work was important partly because of the techniques he introduced—such as the problem box, which he invented and which has since held an important place in animal in-

vestigations; because he demonstrated the possibility of laboratory work on animals; because of the problems he raised; and finally, because of the negative conclusions he drew as to the presence of ideas, reasoning, and imitation in animal learning. To account for animal learning, he introduced the law of effect, according to which it is supposed that the chance associations, if correct, are stamped in by pleasure, and if incorrect, are eliminated by the influence of the resulting dissatisfaction.

In the same year, 1898, two minor studies were published by Kline, of the Clark University Laboratory. One was a sketch of methods in comparative psychology, and the second was an outline for a course in comparative psychology. Another important paper from this laboratory appeared in 1900 and was by Small, who introduced the maze as an instrument for studying animal learning. True, a type of maze had been used by Thorndike, but the pattern introduced by Small is the one that has since become standard equipment in the psychological laboratory.

Another important figure in American comparative psychology is R. M. Yerkes (1876—), whose work, starting about 1900, has run the scale from lower forms to the higher apes and man. Among his important contributions to method are those for studying visual discrimination, which were developed with Watson's assistance; his extensive adaptation and use of the multiple-choice methods; and his more recent methods for the study of anthropoid apes.

One important phase of comparative psychology in America is represented by the work of Margaret Floy Washburn (1871—) whose chief book, *The Animal Mind*, has had editions in 1908, 1917, and 1926. This book represents a frank attempt at a study of the nature and structure of the consciousness of animals, as opposed to a study of learning, discrimination, imitation, and so on *per se*. The movement represented by this book is now dying out.

Such a study is confronted with the extremely difficult task of determining the criteria in terms of which mind in animals can be inferred. Suggestions offered for the solution of this problem have not been lacking. Aristotle implied that the degree of structural and behavioral similarity between man and the animal in question might be taken as an index. Ability to learn was proposed as a criterion by Morgan and Romanes. Darwin apparently used Aristotle's criteria. Loeb proposed "associative memory" as the primary criterion, the presence of which was indicated if the animal could learn. Yerkes, in 1905, submitted these criteria to a searching criticism, pointing out among other things that no animal that has been studied has been shown unable to profit by experience. He suggested six criteria, grouping them under two main heads, as follows: I. Structural Criteria, covering (1) General form of the organism (Organization), (2) Nervous system (Neural-organization), and (3) Specialization in the nervous system (Neural-specialization); II. Functional Criteria, covering (1) General form of reaction (Discrimination), (2) Modifiability of reaction (Docility), and (3) Variableness of reaction (Initiative). But so great are the difficulties involved in arriving at a knowledge of the animal mind, even with these criteria, that psychologists for the most part have turned their energies into other channels.

Another important phase of comparative psychology is the impetus given by it to the rise of behavioristic psychology. This school of psychology was initiated by John B. Watson (1878—) in 1913 and expressed more fully in his *Behavior: An Introduction to Comparative Psychology* (1914), and his *Psychology from the Standpoint of a Behaviorist* (1919), which applied this point of view to human behavior. This school represents an effort to establish a really objective psychology. It is characterized by its attempt to apply that rigid objective method urged by Morgan and Loeb and utilized by workers in physiology.

The work of Franz (1874–1933) and Lashley (1890–) constitutes another important development in comparative psychology. From 1917 till the former's death, they made studies of the exact relationship of brain mechanisms to behavior. Lashley is now continuing the work, and the accomplishments of the two men are well-nigh revolutionizing our concept of neural action not only with reference to the age-old problem of cerebral localization of functions but also with reference to the problems of the laws of learning.

Two important contributions to comparative psychology are found in Russia and Germany. In Russia Ivan Petrovich Pavlov (1849–), beginning about 1903, has contributed a vast amount of work on the conditioned reflex. His work is essentially an attempt to present the physiological principles in terms of which behavior may be adequately explained. The principle of conditioning has been rather widely accepted by American psychologists as furnishing the key to an objective account of behavior, although just at present there are appearing a number of studies in which the adequacy of the concept is being questioned. (See Chapters VI and IX of this book.) In Germany, Wolfgang Köhler (1887–) has led in the study of the higher apes, as has Yerkes in this country. Köhler's important book, *Intelligenzprüfungen an Menschenaffen* (1921), has been translated into English under the title *The Mentality of Apes* (1924). His major contributions consist of the methods he has introduced and the theoretical interpretation he gives to his results. This interpretation harmonizes with the interpretations of Gestalt psychology, which school of psychological thought originated in 1912 at the hands of Wertheimer, Koffka, and Köhler. (See Chapters VII, VIII, and IX of this book.) Both Yerkes and Köhler are employing methods that were used by Hobhouse in some experiments of a similar nature reported in his *Mind in Evolution* (1915).

In closing this summary of the historical development of

comparative psychology, it will be worth while to bring together in a number of statements the chief trends which we have attempted to sketch:

1. In the first place, the field of comparative psychology has come to occupy an important place in its own right. It has come of age, so to speak. Until the Darwinian period, the treatment of animal behavior formed but one phase of the more general treatment or interpretation of nature. It was not then, as it is now, treated as a special and independent field of study.

2. The evolutionary doctrine with its implications, which was earlier a bone of contention among philosophers and scientists, is now a universally accepted view.

3. A most significant change to be noted is the change in the methods of study. The natural history methods are largely of secondary importance at present, while most psychologists are pinning their faith to the experimental and laboratory type of investigation. The anecdotal method is no longer accepted.

4. Correlated with this change is an extension in the type of problems investigated. Previous to the work of Morgan, studies of the instinctive behavior occurring outside the laboratory were typical. While this type still occurs in our own times other problems are now receiving attention. In a count of the number of studies on animal behavior reported in the *Psychological Abstracts* for the years 1931 and 1932, a total of some six hundred titles was found. Besides some 32 general treatises of a somewhat more extended scope, these studies were distributed among the following types of problems: neurological, learning, instincts, higher mental processes, sensory and form discrimination, retention, natural history studies, social activities, and food preferences. This classification, though only roughly approximate, indicates the range of studies now being made. It would be safe to say that every basic or important prob-

lem that has been asked of man's behavior is now being asked concerning the behavior of animals.

5. A controversy that has existed throughout the whole history of the movement and is still alive is that between the vitalists on the one hand and the mechanists on the other, or the vitalistic-mechanistic controversy. The question is whether or not the behavior of animals and men can be explained wholly in terms of physical and chemical principles or whether some other principle peculiar to living organisms must be employed.

6. Two motives have been at work in the study of comparative psychology. The first has for its aim a better understanding of the activities of the animal *per se*; the second, the discovery of principles the knowledge of which will make for a better understanding of human behavior.

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CHAPTER III

Maturation and "Instinctive" Functions

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Introduction

IN a flowerpot sitting on my window ledge there appeared one day half a dozen varieties of seedlings, each of which could be distinguished from the others by the spread of its rootlets, its rate of growth, or slight differences in the hue and texture of its leaves. In my garden is a grafted tree that put forth three kinds of blossoms; from it will come three kinds of plums—yellow, red, and blue—ripening in midsummer approximately three weeks apart. In my neighbor's lot I have observed two species of young fowls that are so different as to vocalizations, resting postures, and modes of feeding that were a magician to give them a common form, size, or coat of feathers, one would never be mistaken for the other.

Since there are no observable differences in the external surroundings of these seedlings in the flowerpot, the branches of the plum tree, and the fowls of the dooryard, we need have no hesitancy, as experimentalists, in assuming that metabolic agencies peculiar to the inner nature of each species have played the dominant rôle in bringing about the gross differentiating features. That is to say, we may take as a working hypothesis, subject to later correction, the view that characteristic features of different species arise from original differences in their genetic con-

stitutions or a long succession of intraorganic controllers of cellular activities, initiated by their genetic constitutions and peculiar to each of the species of plants and animals observed, yet remarkably similar for all members of the same species.

Experimental biologists assure us that there is a hierarchy of internal regulatory factors that control cellular growth and functional organization from the moment the ovum is fertilized until adult life is reached. To development that *primarily* is so regulated, the name *maturation* is given nowadays in order to set it off from other processes by which response mechanisms are acquired, particularly those traditionally designated by the term *learning*.

One or several fundamental methods of development?—Many authors are still uncertain as to whether apparently different types of development really differ from each other along fundamental psychobiological lines. However, in the interest of clearness, now, as heretofore, they sometimes proceed as if types could be distinguished both on logical and on fundamental grounds. Particularly is this true of action systems attaining specific and precise relationships with one or more of a large class of objects or patterns of stimulation acting either from within or from outside the animal's body. Such distinctions usually indicate to the reader what topics are momentarily under discussion and, like other provisional definitions, may be discarded when that purpose has been served.

Since different opinions are to be found as to what kinds of development properly fall under the heading *maturation* and what kinds under the term *learning*, I believe that our present needs can best be served if we avoid distinctions that are too finely drawn. Accordingly, let us say that, in the most typical instances, the term *learning* will be used to designate *individual* acquisition in which response mechanisms are organized and dependent relationships established between these mechanisms and relatively specific,

ofttimes repetitive patterns of stimulation impinging on receptors either from within or from without the body of the *individual*. The organization of these mechanisms seldom precedes and apparently grows out of the biological needs that they serve; and never are the mechanisms transmitted from parent to offspring in ratios typical of hereditary traits. One or two illustrations, even though given somewhat dogmatically, will help to make our meaning clear.

Through *maturational* development, young dogs are capable of micturition at the time of birth or even slightly before; but only a few of all the dogs in the world, and these at quite variable times and in response to repetitive patterns of stimulation, *learn* that urine must not be voided in the domicile of man. Such sanitary habits of parent dogs are never inherited by their offspring.

Similarly, as a result of *maturational development* newborn lambs acquire the sucking response that enables them to take milk from a large class of nipple-like containers; yet, seldom indeed does a specific lamb *X*, when beyond a day or two of age, attempt to obtain milk from anything but a bottle or a specific lactating mother *Y*, which it *learns* to identify, to follow, and to pick out from among other adults of similar appearance.

No doubt, the critical reader will find instances in which the foregoing provisional distinction between maturation and learning breaks down. But, as our chapter unfolds, the reason for this fact and possibly the remedy as well will become apparent.

Structural and functional development are inseparable.—From the very beginning maturational development proceeds simultaneously along structural and functional lines. At a given moment, however, *form* or *mass* in an organism may attract the attention of one biologist and *acceleration of cell division* that of another biologist, while a psychologist may have eyes only for *movements* of the body or some

of its appendages. At the same time, experimenters working together on this animal could readily detect examples of any and all of the familiar phenomena that one is accustomed to classify under the conventional rubrics: biophysics, biochemistry, morphology, physiology, and psychology. Moreover, a view that projects into animals, themselves, that degree of separateness or dissociation of vital processes wittingly implied in classroom discussions, places a stumblingblock in the way of students who would obtain an accurate conception as to how animals really progress from one to another stage on the long developmental road leading to adulthood.

Our point of departure.—Anatomists use such terms as cleavage, segmentation, gastrulation, and so on to designate typical early developmental processes. Also, it is their custom to describe embryos in which a specific number of somites can be seen. Still later, when somites no longer provide the differentials, crown-rump length, birth (or its equivalent in nonmammalian forms), number of teeth, ossification centers, signs of pubescence, and so forth, are used as convenient landmarks for descriptive accounts. For the genetic psychologist, initial response has always been a favorite point at which to begin record taking, and this will be our present point of departure. During the pre-activity stage, there is no evidence of learning, as we have defined this term. Therefore, by inference, we may look upon development prior to bodily movement as purely maturational in type.

With initial responses, certain perennial troubles confront us, because movements usually are crude and weak in their beginnings but, with time, become strong, precise, and specific in direction. How to credit this improvement, whether to maturation, to learning, or to both, and if the latter, in what proportion, is a difficult problem. Theorists have wrestled with the question in the dark for years without making substantial progress toward its solution, but now

in experimental psychology for the first time a new approach to the problem is beginning to yield invaluable returns. To the experimentalist, the problem is not so much one of classification as one of determining as exactly as possible what forces of the internal and external environments provide the major controls for species and individual development and what agencies mobilize the action systems by which life is maintained and the continuity of the species is assured. More specifically, the problem resolves itself into the following types of inquiry, all of which are amenable to experimental study:

1. What specific unlearned responses or clusters of unlearned responses are functionally associated with the fundamental biological needs?

2. What is the genetic history of unlearned action systems and what are the internal biological needs by which they are activated?

3. By what incentives can unlearned responses be evoked? What additional stimuli of an equivalent nature can with training be substituted for those originally adequate?

4. What laws, or bases for prediction, can be derived from the study of vigor of response in relation, on the one hand, to changing values on the scale of biological needs, and, on the other hand, to type of incentive or rewards for action?

The Ontogenesis of Unlearned Behavior

Like organs of the body, initial responses in embryos, foetuses, or postnatal young make their advent in a sequential order and with temporal spacing that is highly characteristic of the species. For instance, chicks, ducks, turkeys, and quails pick up small seeds by pecking soon after they are hatched; but sparrows, robins, and pigeons can do no better than extend their necks and hold their mouths agape to receive soft foods from the parents' bills.

Guinea pigs, rats, and rabbits have action systems that permit of breathing and righting slightly before they are able to obtain milk by sucking; but young opossums breathe and maintain themselves by sucking some six weeks before they assume the characteristic adult posture. Rabbits locomote by hopping about 12 days after birth, and children creep approximately 1 year thereafter; whereas a young colt or guinea pig can walk, trot, or gallop within a day or two of its first birthday. In short, wherever the student of nature casts his glance about him, he may see evidences of sequential order and temporal spacing that tend to differentiate one species from another. Upon considering the following or similar illustrations, the student will see for himself why orderly development in young animals has always held in the opinion of man a high place among the many wonders of nature.

Developmental sequences and schedules exemplified.

(1) *Fœtal and newborn rats.*—By breeding receptive rats, it is possible to date the time of conception with only a few hours of experimental error. Counting from the hour of breeding, the first movement of fœtuses appears shortly after they are 14 days old, and if at this time a pregnant female is properly anæsthetized, the fœtuses may be removed from the amniotic cavity and immersed in a saline solution of approximately the same temperature as the amniotic fluid, still obtaining their oxygen and food supply through the placentas, which in this experiment should not be detached. If this is done, one may observe or stimulate the fœtuses to determine when spontaneous movements or responses to external stimulation make their appearance. Taking the work of Angulo ^{(2)*} as our source of information, we have constructed a chart of the rat's developmental schedule up to birth. Studies of Small ⁽²²⁾ and others provide additional data for the period of post-natal development.

* Numbers in parentheses refer to Bibliography at end of chapter.

Referring to Figure 1, the reader will see that the growth of responses in the foetus is very gradual. The wave of growth continues well out into postnatal life without any significant change to mark the time of birth. Although individual differences are clearly evident at all stages of development, so small are they in amount, as compared with those of species, that one may liken them to barely visible ripples appearing on the crests of giant billows. A survey of these responses in relation to the animal's postnatal needs for independent existence indicates that functional utility (not always functional maturity) appears in action systems somewhat in advance of the need they are destined to serve. Although in their first manifestations action systems may be weak, erratic, and nonspecific, strength, precision, and specificity come with time, even though opportunity for practice, in the usual sense of that term, is not given. The order of appearance of responses seems to run in a head-to-foot direction and from centrum to periphery so far as the trunk and the appendages are concerned.

Without attempting to ascertain what further information we may glean from the foregoing illustrative case, let us hasten on to other illustrations, particularly those that will provide us with contrasting materials for later discussions.

(2) *Fœtal responses of guinea pigs*.—The following items roughly depict behavioral growth in prenatal guinea pigs experimentally removed and detached from their mothers by Avery⁽³⁾ when they were between 45 and 68 days of age, the latter being the end of the gestation period. At 45 days or earlier, a few respiratory gasps were to be seen, and irregular breathing appeared in those of 50 to 60 days of age; regular and continuous breathing was found after the 64th day. On the 48th day, kicking or withdrawal responses followed upon pinching the skin of either foot. On the 50th day, the first spontaneous kicking movements

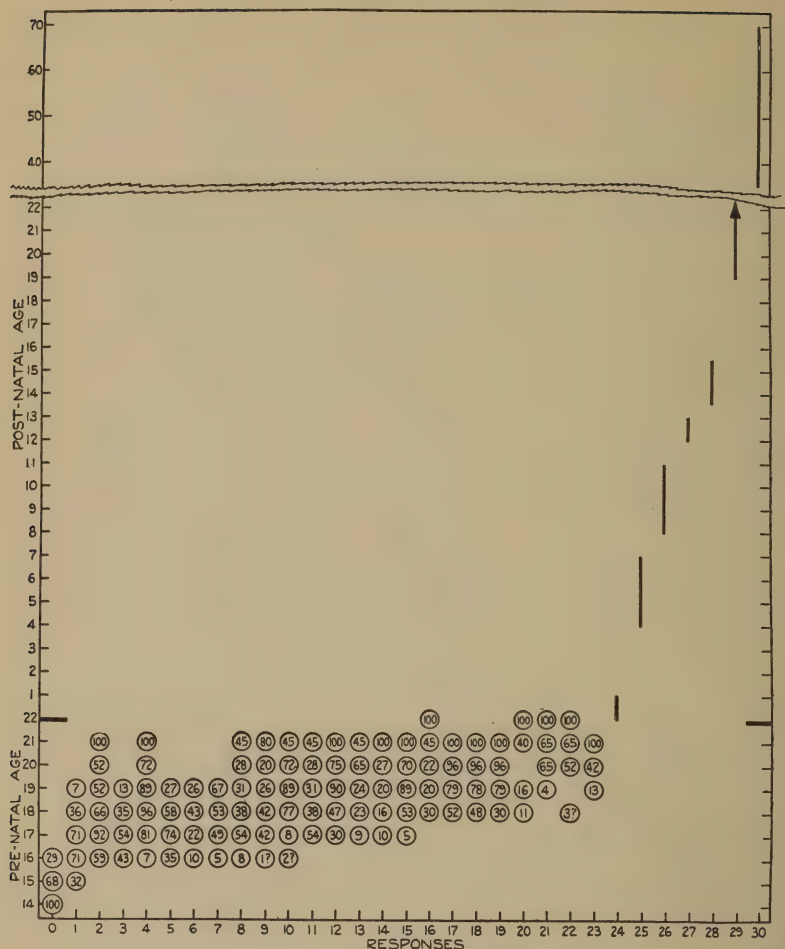


Fig. 1.—Illustrating the growth of responses in the prenatal and postnatal albino rats. Data for the prenatal period, 14 to 22 days, are based on the extensive observations of Angulo,⁽²⁾ who observed the following numbers of foetuses of the ages 14 to 21 days respectively: 59, 63, 150, 93, 70, 90, 98, 20. (Gestation period, 22 days.) Data for the postnatal period are based on observations by Small⁽²²⁾ and the present author. The numbers enclosed in circles indicate the percentage of each group displaying the response indicated by the code numbers on the abscissa. Vertical lines at right of the diagram indicate the approximate age ranges

at which postnatal responses, indicated by code numbers at the bottom of the diagram, are first manifested. Percentages for each age can be given only for the reproductive responses, and these vary somewhat according to the diet used. Numbers at the bottom of the diagram refer to the following responses:

- | | |
|--|--|
| 0. Non-motile. | 13. Attempts to assume " <i>the optimum physiological posture.</i> " |
| 1. Lateral flexion of trunk. | 14. Independent movement of hind limbs. |
| 2. Lateral flexion of trunk with movement of fore limbs. | 15. Extension of head and rump with kicking of hind limbs. |
| 3. Lateral flexion of rump. | 16. Independent opening of mouth. |
| 4. Extension of head. | 17. Independent extension of hands. |
| 5. Extension of head with opening of mouth. | 18. Independent flexion of hands. |
| 6. Extension of head with opening of mouth and protrusion of tongue. | 19. Specific reflexes. |
| 7. Lateral flexion of rump with movements of hind limbs. | 20. Movement of tail. |
| 8. Ventroflexion of trunk and rump. | 21. Independent movement of feet. |
| 9. Independent movement of fore limbs. | 22. Independent movement of tongue. |
| 10. Maintained contractions. | 23. Independent closing of mouth. |
| 11. Contraction of abdominal muscles. | 24. Rolls from back to belly. |
| 12. Extension of rump. | 25. Crawls rapidly. |
| | 26. Washes face; sits on haunches. |
| | 27. Responds to noises. |
| | 28. Eyes open. |
| | 29. Eats solid foods. |
| | 30. Initial sexual responses. |

For a discussion of the fact that some responses appearing early are not observed in the older fetuses, see the original paper by Angulo.⁽²⁾

were observed. Eyelids opened between the 55th and the 57th days. On the 57th day, kicking responses to pin-pricks and likewise eyelid reflexes to air blown on the cornea could be elicited. Vocalizations were made by those of 58 days; scratch reflexes with the forepaws came on the 59th day. On the 60th, the pig crawled and rolled from back to side or over to its feet; it also gave a twitch of the ear to auditory stimuli. Spontaneous scratch reflexes with the fore limbs appeared on the 61st day. On the 63rd day, the pig could stand and walk. On the 65th day, the sucking response was made to the mother's nipple, and individuals of this age could maintain themselves on milk

taken of their own initiative from lactating mothers. On the 67th day, nosing of objects, chewing of paper, shavings, and alfalfa hay were seen in pigs soon after they were delivered from the mother.

Avery voiced the query as to whether postures assumed by the mother during the latter days of the gravid period provided the adequate stimulus for young pigs of 63 days or more to shift their positions continually so that their backs were up and their feet toward the surface of the earth. To test this point, radiographs of pregnant females held in various positions were made (e.g., back down, back up, on right side, and on left side). In one series of tests pregnant females were shifted at five-minute intervals during a 30-minute period, and radiographs were made before each shift. The young kept their original positions throughout the 30 minutes. Radiographs showed foetuses of the same litter in various positions, which fact strongly suggests that prior to birth they do not practice spatial orientation in response to shifts of the mother's position.

(3) *Fœtal and newborn rabbits*.—The rabbit, having a relatively short gestation period (30 days), provides an excellent contrast for rats and guinea pigs. If the foetuses are removed from the mother from 3 to 4 days before the end of the gestation period, they move the trunk and limbs spontaneously or in response to mechanical stimuli applied at various points on the body. At 26 days, respiratory movements are not yet adequate to support life for more than a few seconds, if at all, but with each succeeding day of intrauterine life they become more and more serviceable. Within a day or two of birth, the foetus is capable of crawling, righting itself, and sucking from the mother's nipple. None of these responses, however, are as vigorous or precise as those of the newborn, which fact goes to show that functional maturation proceeds at a rapid rate during the later days of gestation. Figure 2, based on work of Kao,⁽¹⁴⁾ illustrates the ages at which other responses of post-

mother's cloaca to her pouch by grasping abdominal hair between the toes of its forelegs. Wide, sweeping movements of the head from side to side enable it to contact a nipple in the pouch whereon it holds with great tenacity. So excellent is the junction of mouth and breast that lay traditions inform us that young opossums grow from the breast of the mother. At birth the young responds to cutaneous stimuli applied to various parts of the body, but most specifically to those applied on the face. As yet, however, they cannot right themselves when placed on side or back, have none of the defensive movements exhibited by young guinea pigs from 7 to 8 days prior to the time of birth, and can perform none of the more complex locomotor movements exhibited by newborn rats, kittens, guinea pigs, puppies, calves, colts, sheep, and dozens of other well-known animals. (See Figure 3.)

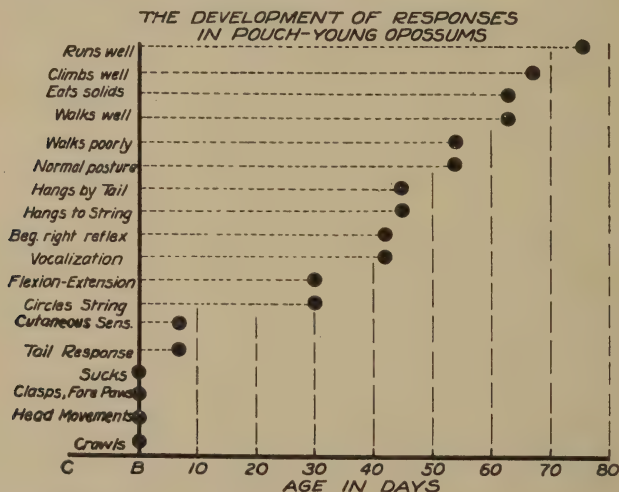


Fig. 3.—Development of responses in pouch-young opossums. The heavy dots indicate the approximate ages at which responses at the left are manifested. More extensive investigations will cause these dots to shift slightly to the right or to the left, but the general trend of results will probably stand as given in this pioneer study, based on only a small number of cases. (After Langworthy.⁽¹⁶⁾)

At 1 week of age, the forelegs beat in such a manner as to insure progression, if the claws catch onto solid objects, but the hind legs are still more or less useless. The tail responds to cutaneous stimulation and acts as a prehensile, grasping organ, although it lacks sufficient strength to support the weight of the young. Thermal and tactile stimuli arouse local responses from all parts of the body, and at this time the young will crawl away from cold and toward warm objects. The eyes are not yet open, no response is given to auditory stimuli, and righting reflexes are not present.

At approximately 1 month of age, the young still lie upon their sides because the righting reflexes are absent. The hind limbs move more than during the first week, but their movements, as yet, are not well coördinated with those of the fore limbs. They grasp a suspended thread with the fore toes but circle the thread rather than climb it.

By the end of 6 weeks, many responses previously displayed have become more precise and some that formerly appeared uncoördinated have now become an integral part of well defined movements. Immature righting reflexes are manifested at this time; when put on its feet, the animal can take two or three steps before falling over upon its side. Vocalizations now are made. At the age of 46 days, the animal can support its weight by grasping objects with its tail. At 54 days, it assumes the normal standing posture. Now it climbs a rope and crawls quite well, but with legs sprawled out. At the end of 9 weeks, the young can walk and eat solid food. Climbing and running are well done at the age of 10 weeks, when, for the first time, one can say that the motor abilities are on a par with those of young guinea pigs or rats that are in the second or third week of postnatal life.

Extensive histological studies of the central nervous system of the pouch-young opossums, and similar studies of rats, kittens, and children, do not give conclusive evidence

that growth of behavior is dependent upon myelinization of nerve tracts within the cord or brain stem. Much coordinated behavior antedates myelinization in all of these species of animals.

(5) *The human foetus and infant.*—Probably no animal has a more highly standardized or longer course of prenatal and postnatal development than the human infant. The philosopher Fisk made the brilliant remark, in substance, that man has a longer period of infancy than the lower animals because he has a higher destiny to fulfill. No animal surpasses man as to psychomotor development.

A small number of selected items will serve to illustrate the detail with which experimentalists now are working out schedules of development in the human infant. In Figure 4 are illustrated certain stages of infant locomotor development as worked out by Shirley.⁽²¹⁾ This diagram and other diagrams not reproduced herein indicate that the earliest responses pertaining to locomotion, such as chin movements, chest raising, sitting, knee pushing, and so on, make their appearance long before sitting alone, creeping, standing alone, and walking without support.

Shirley states that locomotor development

. . . follows a pattern that has five major orders. They may be described more or less adequately as: (a) development of passive postural control; (b) development of active postural control; (c) active efforts toward locomotion; (d) locomotion by creeping and walking with support; (e) walking alone. Each major order of development has several stages. There is some shifting in sequence of stages within an order, but there is no transposition of a stage from one order to another. (Page 193.)

Intensive studies of the growth of behavior in the human foetus, the infant, and the child clearly suggest that man differs from all other anthropoids even more radically in his mental developmental schedules than with respect to the more obvious morphological characters so strikingly apparent even to the unschooled eye.

Characteristics common to all development in animals.—A comparative study of the conditions under which each of the foregoing species grows to adulthood reveals certain common characteristics, of which the following items are among the most apparent.

(1) Development of any animal from the fertilized ovum to adulthood is contingent upon its having around it a regulated or standard *ensemble* of external forces of nature, in which such things as organic and inorganic nutrients,

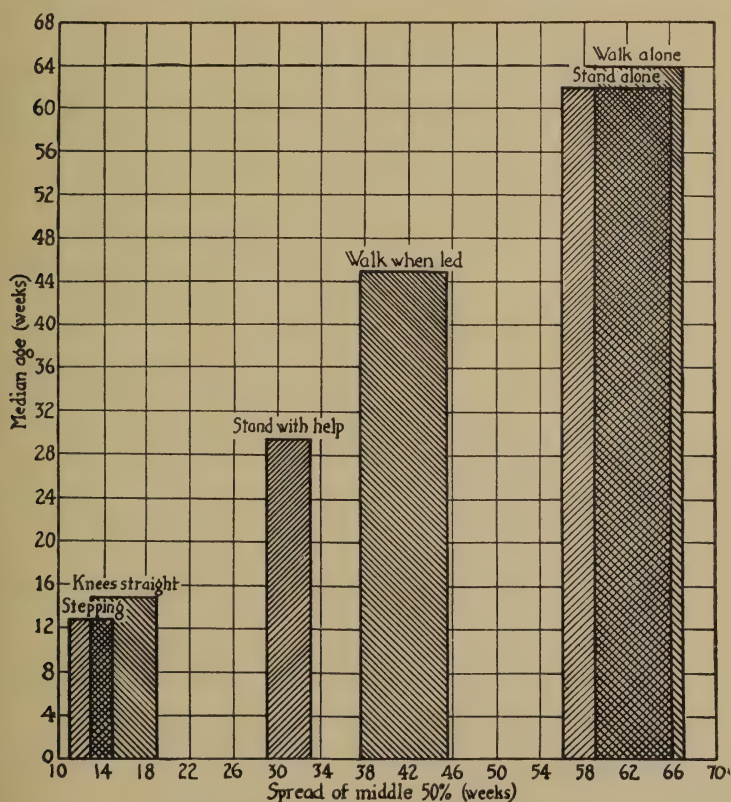


Fig. 4.—Progress Toward Walking. (After Shirley.⁽²¹⁾ Reproduced by permission of the University of Minnesota Press.)

oxygen, water, and temperature fluctuate between limits narrowly defined for a species or a few closely related species.⁽¹⁶⁾ The standard *ensemble* varies greatly for distantly related groups—a fact that may, in part, account for many characteristic differences between species.

(2) Sequence and temporal intervals between initial responses are no less characteristic of a species than are the morphological characteristics on which our present nomenclature is based. Give me the number of days between time of conception and birth in 100 each of normal rats, rabbits, guinea pigs, horses, and human babies, and I shall segregate these animals with no per cent of error; state how long it is from the date of conception before the young take milk by sucking, assume the adult posture, perform the first fruitful reproductive act; or even give me the temporal interval between initial appearances of any pair of the foregoing acts, and I shall segregate the young with almost the same high degree of accuracy one expects of those relying upon well-known morphological differences.

(3) Orderly growth of responses in organisms occurs simultaneously on many frontiers and serviceable maturity of action systems is attained prior to the time they come into the service of fundamental bodily needs. Without benefit of practice, as that term is ordinarily understood, structural mechanisms become integrated in immobile embryos just as later in the active organism they seem to appear without necessary practice or training. And despite community of living, immature young that develop equivalent reaction mechanisms to serve equivalent bodily needs, do not lose the typical developmental schedules and sequences by which their respective species are characterized.

Such facts as the foregoing constitute strong presumptive evidence for the *maturational* hypothesis of early development in animals. Intraorganically regulated development provides each species with action systems and the biological

fundaments of constant or intermittent physiological states out of which instinctive reactions, insight reactions, and habits are formed.

On the Trail of Developmental Controls

If we are to discover the mechanisms that control behavioral growth, it is necessary to observe cases in which one or more agencies suspected of having a regulatory influence are inoperative or effectively controlled. That is to say, *we must look for effective variables operating in an otherwise standard matrix of dynamic factors*. Although numerous examples of control have been cited by experimentalists, they are scattered among various species of animals; hence only a patchwork sketch for a single species can as yet be given.

The yucca moth.—Perhaps no instance more dramatically illustrates the operation of intraorganic controls in maturational development than that of the yucca moth, so beautifully described by Lloyd Morgan.⁽¹⁷⁾

The silvery, straw-colored insects emerge from their chrysalis cases just when the large, yellowish-white, bell-shaped flowers of the yucca open, each for a single night. From the anthers of one of these flowers the female moth collects the golden pollen, and kneads the adhesive material into a little pellet, which she holds beneath her head by means of the greatly enlarged bristly palps. Thus laden, she flies off and seeks another flower. Having found one, she pierces with the sharp lancets of her ovipositor the tissue of the pistil, lays her eggs among the ovules, and then, darting to the top of the stigma, stuffs the fertilizing pollen-pellet into its funnel-shaped opening.

These visits of the insects are necessary for the pollination of the flower, which is accomplished by no other insect and by no other method. Likewise the fertilized ovules are necessary for the growth of yucca larvæ when they emerge from the eggs in four or five days. After eating some of the tender ovules, the larvæ cut holes through the ovary,

spin webs, descend to the ground, burrow beneath its surface, and pass the winter there in the pupal state, from which they emerge at the time the yucca is in flower. The adult does not partake of the pollen which it gathers and probably obtains no nourishment at all from the plant while performing this round of complicated activities. Finding the flower is itself an unlearned response, a type of chemotropism so common among insects. The adult insect does not learn this complicated routine of acts through imitation of its parents, long since dead, or contemporaries either, for its visual receptors do not provide the kind of vision necessary to the human's concept of visual guidance. Action systems of the larvæ are totally unlike those of adults, and the activities are even performed with different appendages; the body of this selfsame larva that descended the silken thread to bury itself in the ground is dedifferentiated and resynthesized during the resting state; finally, a prolonged interval of time, the winter season, intervenes between the last act of the larva and the first of the adult. In view of these facts, no concept of memory or transfer of training that is supported by experimental evidences can be invoked to account for the behavior of the yucca moth. We are merely moving along lines being supported more and more by experimental data when we say that intra-organic controls are probably responsible for the organization and energizing of this cluster of ordered responses, appearing as they do only after a prolonged resting period, near the end of the individual's life span, being functionally similar or equivalent for all members of the species, and differing in essential ways from the reproductive behavior of other moths, beetles, and so on.

Examples of similar unlearned responses might be gathered by the hundreds from the writings of entomologists to illustrate the marvelous aptitudes for complex responses first displayed by bees, wasps, moths, and other insects immediately after they emerge from their last molt. Different

species of insects, sheltered and nourished by the same plant or animal, lay their eggs in the same sheltered nook; but each egg, in its own time, yields a larva that feeds selectively, responds characteristically to light, shadows, odors, and tactual qualities of surfaces, molts at specific times, and eventually emerges as an adult by crawling, hopping, or flying. Neither larvæ nor adults of the class Insecta have shown great educability at the hands of man or in their native habitats, so far as experimentalists know; hence we are merely keeping our feet on the ground of evidence, going to the incompletely known from established facts, when we say that intraorganic factors of control, acting in a standardized matrix of dynamic factors, provide insects with most of the marvelous aptitudes for response everywhere exhibited about us.

"Synthetic" queens among the honey bees.—Variations in developmental trends are sometimes initiated by factors located outside the body of the organism. So far as the author knows, however, these alterations are productive of individual differences within a species rather than species differences, and many of them are not transmitted as heritable characters. The following illustration will illustrate the idea.

As is well known, one of the chief duties of young worker bees is that of feeding the larvæ. The eggs hatch in about 3 days, whereupon there lies at the bottom of the cell a worm-like creature so helpless that food must be forced into its mouth by the nursemaid workers. At first all of the larvæ receive a predigested substance that is forced from the stomachs of the workers and known as "royal jelly." After about 3 days, most of them are given bee-bread, which is a mixture of honey and pollen, but a few are given an enlarged cell and fed on "royal jelly" throughout the larval state. The latter become the queens and the former the workers. Should accident befall developing queens, the nursemaid workers enlarge the cells of worker

larvæ, just recently put on the diet of bee-bread, and restore their menu of "royal jelly." If development has not already gone too far, some of these larvæ grow to resemble the more common queens, which were never fed anything but "royal jelly." "Synthetic" queens, like all queen bees, differ from workers in size, in form, and in primary and secondary sexual characters. Upon emerging from the larval state, they perform reproductive functions rather than the diverse menial labors of workers. These facts indicate that during the first 3 or 4 days of life, a female larva has the capacity of developing into either a queen or a worker, the course of somatic development and behavioral growth being wholly determined by adult members of the hive and regulated by nutritional factors.

Correlated neuromuscular development and behavior in amphibia.—Numerous highly technical studies by Coghill^(8, 9) have correlated neuromuscular growth and integration of behavior patterns in amphibian larvæ. Only by referring to his original papers can one obtain a correct impression of the great wealth of detail he has provided that go to show that behavioral growth is truly an expression of neuromuscular growth, and that *integration of action systems is primarily regulated by factors inherent within the organism from the very beginning of its development*. The following quotation indicates his conclusion as to how patterns of behavior are acquired in the early stages of larval development. Coghill says,

The growth of the nervous system, insofar as it has been definitely correlated with the development of the behavior pattern, demonstrates that fractional patterns (reflexes) arise by a process of individuation within a primarily integrated total pattern, and that the latter does not arise by an integration of independent reflexes. The form of the behavior pattern in *Amblystoma* up to and including locomotion is determined by specific neural counterparts that acquire their specificity in functional value through laws of growth in the nervous system. There is evidence also that mechanisms that condition the performance of such a behavior pattern as locomotion in mammals are determined in the

same manner. It is important, therefore, to know how far growth, in the sense of the differentiation of new functional parts of cells, is projected into the life-history of the vertebrate, for so long as it continues it must participate in the function of the nervous system as a whole and, therefore, in the development of the behavior pattern.

Continuing the work of Coghill is the comprehensive study of Tracy⁽²⁸⁾ on the toadfish. He observed the patterns of bodily movement from their initial appearance in the embryos through successive stages until the animals became free-swimming. His correlated studies of neuromuscular development and behavior led to the belief that differences in reactions displayed at different stages of development arise from temporal differences in the establishment of effective connections between various elements of the embryonal nervous system (primitive bilateral motor system, commissural elements, spinal ganglion cells, Rohn Beard cells, and receptors). He supports the view of Coghill that integration of behavior patterns is primarily regulated by intraorganic factors of control that manifest themselves structurally long before the initial movements of the embryo are seen.

Hastening metamorphosis in amphibians.*—Alterations of time relations in the development as well as in the sequential order of responses can be produced by varying the environments in which specific potentialities of the genes are realized. The following quotation from a study by Jennings⁽¹³⁾ beautifully illustrates the point.

In that group of the Amphibia which includes the toads and frogs, at a certain period the tail and gills are lost, legs develop, there is an internal and external transformation, and the tadpole metamorphoses into the four-legged frog or toad. What brings about this metamorphosis? J. F. Gudernatsch found that if very young tadpoles are fed pieces of the thyroid gland, they quickly metamorphose into frogs, even though as yet extremely small. In this way frogs as small as flies were produced. Tadpoles of the bullfrog, that usually do not metamorphose

* See Chapter V for additional discussions.

till two or three years old, were thus caused to metamorphose during the first season of this existence, and within two weeks of the time that the feeding of the thyroid was begun. . . . The thyroid gland produces an inner secretion, or hormone, that contains iodine, and that passes into the blood and so circulates through the body. The iodine that it contains is united with certain organic compounds, and some of the effects of its secretions are not producible by iodine alone; this is particularly true of its effects in higher animals. The thyroid, like other parts of the body, develops gradually, and in the early stages of its development it does not produce its secretion. It remains thus inactive even past the time when the remainder of the body has become capable of reacting to its secretion. But at a certain period it begins to produce its characteristic secretion, and to pour it into the blood. And as a result the tadpole transforms into the frog or toad. (Page 113.)

Needless to say, functional metamorphosis goes hand in hand with the structural metamorphosis* of which Jennings is chiefly talking in the foregoing quotation. Further on, Jennings says,

The effect of the thyroid hormone thus differs greatly in different animals. The cells in different species have different constitutions, diverse genes; and they react diversely to the same hormone, just as diverse parts of the same individual react diversely to the same hormone. The effect produced depends as much on the constitution of the cells acted on as it does on the nature of the hormone. (Page 117.)

Temperamental traits in relation to genetic constitutions.—If one breeds domestic albino rats taken from a strain known for its gentleness and within the same half-hour or so breeds the same females to trapped wild males, a certain number of mixed litters may be expected. The pure albinos are readily distinguished from the half-breeds because all of the latter have brown hair. Although the albino mothers are allowed to suckle the young in the usual way, and after weaning all are treated alike and finally

* The secretion from the anterior lobe of the hypophysis is an activator of the thyroid and thus plays an important role in the metamorphosis of amphibia. See Chapter V, by Moss.

tested by the same person without reference to coat color, quantitative differences in wild and savage behavior will be readily seen. The manner of siring the litters as well as the subsequent treatment of the young point to the genetic constitution of the males as the primary cause of temperamental differences developing in the offspring. Had wild mothers been used instead of tame albinos, the absolute differences in wildness and savageness might have been somewhat different from those obtained in the experiment described above, for it is not improbable that the blood stream of the mother and her attitude toward the young contribute something to their temperaments. Yet a positive finding of this kind would not negate the substance of our original conclusion, for we have merely suggested that the *difference* between albinos and half-breeds is to be attributed to intraorganic factors. The latter have caused albinos and half-breeds to utilize differently the maternal environment in which they were placed.

If fertilized ova from full-blood wild rats could be successfully implanted into the reproductive tracts of tame albino rats and allowed to placentate and develop as though they had come from the ovaries of the albino, and then if the same kind of experiment were repeated with wild females substituted for the albinos, a great deal might be learned concerning the relative contribution to temperamental differences made by the blood stream of mothers, conceived as hosts, on the one hand, and the genetic constitutions of the young, on the other. Such an experiment is not at all impracticable.

Puberty may be delayed, accelerated, suppressed, or altered by nutritional or glandular influences.*—Time upon time, the initial appearance of sexual behavior in rats and other laboratory animals has been delayed or accelerated almost at will by the deprivation or by the liberal supply of one or more of the animal's nutritional require-

* Additional data are given in Chapter V.

ments for normal physical growth.^(1, 24) Likewise, when vertebrates are deprived of the gonads or the anterior lobe of the hypophysis at an early age, neither primary nor secondary sexual behavior is seen in those individuals reaching adult life.⁽¹⁾ On the other hand, if gonadal secretory products or hypophysial hormone be injected into very young individuals, puberty *præcox* with precocious sexual behavior will ordinarily follow. In such cases we alter the temporal intervals in schedules and change sequences both by displacement and by dropping out responses from the total repertoire.

In this same connection we may mention the interesting cases of sex reversal appearing in fowls and sometimes in mammals. Crew⁽¹⁰⁾ described a case of complete sex reversal in a hen that formerly had laid eggs, incubated them, and brooded chicks. Subsequently this same animal suffered loss of ovary through disease. Tissue from the genital ridge gave rise to new testes, which in turn brought on the fundamental characteristics of a cockerel. By castration of 1-day female chicks, sex reversal in various stages of completeness may be produced.⁽¹⁾ Beyond a doubt much of the sexual dimorphism of wild birds, which is paralleled by differential sexual behavior, is correlated with gonadal secretions.

Some variables are related temporally but not causally with developmental sequences and schedules.—The determinative agencies responsible for early histogenesis and organogenesis in embryos are known to act very early in the course of ontogenetic development, as is demonstrated by much brilliant work on homeo- and hetero-transplantation of tissues, limb buds, sections of the central nervous system, or receptor mechanisms in living embryos.⁽¹¹⁾ In all probability the same can be said, with certain reservations, for behavior patterns as well, because behavior is so intimately correlated with somatic development. The

anlagen of behavioral patterns are laid down long before the patterns make their first appearance; and maturational development, made possible by highly standardized environments common to the species, carries these potentialities along to the stage of fruition seen in the more advanced stages of embryonal or foetal behavior.

This point of view provides us with a proper basis for understanding the acquisition of adult behavior mechanisms in insects during the pupal stage and likewise for understanding the results from experiments such as those reported by Carmichael,^(6, 7) who brought eggs of the frog and salamander into the laboratory to develop under conditions suitable for special observation. A number of embryos in their early head-bud and tail-bud stages were divided into control and experimental groups. The controls were allowed to develop in tap water, a satisfactory medium for normal growth and activity, whereas the experimental group was put into a chloretone solution of just sufficient concentration to keep the developing larvæ in a state of anæsthesia without injuring the developing structures. When the controls had reached a free-swimming stage, the anæsthetized individuals were transferred to tap water to recover from the narcotic. Also, some of the controls were anæsthetized just prior to testing of the experimentals, and then released into fresh water for comparison with the experimentals. The net result of this experiment is indicated by the following quotation:⁽⁶⁾

In fact a number of the eighteen *amblystoma* embryos swam so well in less than one-half hour after they had shown the first sign of movement, that they could with difficulty, if at all, be distinguished from members of the control group who had been free-swimmers for five days. (Page 55.)

The rate of recovery of the experimentals and the narcotized controls was said to be the same. All together, the results may be taken as presumptive evidence that mat-

urational development, rather than learning, as we have used that term, accounts for the free-swimming responses of these amblystoma. Furthermore, it may be assumed that *use* of the locomotor equipment, gradually acquired by the control group, was not an *effective variable* so far as maturation of the locomotor system was concerned. Temporal relationship is always to be distinguished from causal relationship in maturational development, for as a general rule the effective organizers have done their work well in advance of the time that their influence may be detected in resultant behavior mechanisms.

Interdependent Relationships between Maturation and Learning

Although we have declared our ignorance as to whether maturation and learning are fundamentally different biological processes, we have made verbal distinctions between them and now it remains for us to point out certain important dependent relationships between maturational level and learning rate and likewise between specific individual habits and maturational rates.

Modifiability in relation to the age factor.—Stoltenberg ⁽²³⁾ rotated young pigeons on a turntable at the ages of 5, 10, 20, 35, and 90–120 days. Each bird was tested on 10 different occasions, with the direction of turning alternated on successive trials. Each complete trial consisted of 10 turns of the table in a 20-second interval, and successive trials were administered every two minutes. In Table I will be found the average number of nystagmic movements made by birds of each age group on the first and last pairs of trials. Table II gives similar data for the duration of nystagmic movements following each trial. From a consideration of these tables, it will be seen that there is an increase in both the number and the duration of movements up to the age of 35 days, or the approximate time young

TABLE I

AVERAGE NUMBER OF POST-ROTATIONAL NYSTAGMIC MOVEMENTS
IN DIFFERENT AGE GROUPS OF SQUABS
(From 14 to 16 Birds Were in Each Group)

<i>Rotations</i>	<i>Ages of Groups</i>				
	5 <i>Days</i>	10 <i>Days</i>	20 <i>Days</i>	35 <i>Days</i>	90-120 <i>Days</i>
1 and 2	4.29	14.35	24.89	33.20	32.95
9 and 10	4.65	10.53	17.33	20.97	21.85
Decrease	-36	3.82	7.56	12.23	11.10
% Decrease	-8.40	26.60	30.30	36.90	33.80

TABLE II

AVERAGE OF THE TIME (SECONDS) IN WHICH POST-ROTATIONAL NYSTAGMIC
MOVEMENTS WERE OBSERVED IN DIFFERENT AGE GROUPS OF SQUABS
(From 15 to 16 Birds Were in Each Group)

<i>Rotations</i>	<i>Ages of Groups</i>				
	5 <i>Days</i>	10 <i>Days</i>	20 <i>Days</i>	35 <i>Days</i>	90-120 <i>Days</i>
1 and 2	3.66	10.75	19.11	23.59	23.56
9 and 10	3.67	8.07	13.68	16.20	17.13
Decrease	-.01	2.68	5.43	7.39	6.43
% Decrease	-27	25.8	28.4	31.40	27.30

squabs leave the nest; also, and what is more important for our present interest, there is a gradual decrease in both the frequency and the duration of movements associated with training on the turntable up to the age of 35 days, after which age differences are not found. The cause for this differential modifiability with age is by no means fully understood as yet, but it seems not improbable that it is brought about almost wholly by maturational factors. Opportunities to profit by experience similar to or equivalent to that provided by the turntable are certainly very meager if not totally absent in nestling squabs.

Quantitative study of improvement.—Bird ⁽⁴⁾ has repeated and greatly extended the classical experiment of Breed and Shepard ⁽⁵⁾ on the improvement of feeding re-

actions in chicks with age and with practice. Noteworthy are his more elaborate system of controls and the increase in numbers of subjects tested. Among his conclusions are the following:

The most rapid increase in accuracy of swallowing gains occurs during the three initial practice days, whether these three days immediately succeed the time of hatching or come after a period of artificial delay. A part of the increase is attributed to general physiological development, which occurs during the first few days of postnatal life, irrespective of practice in pecking. Delayed practice is followed by accuracy of swallowing which at the initial test is no greater than that observed in one-day-old animals.

Another investigation on accuracy of pecking in chicks was reported by Mosley.⁽¹⁸⁾ She verified the data of Breed on the relatively complete development of the pecking response at the time of hatching, but found a decrease in the rate of improvement of the pecking response in chicks fed artificially for various periods of time after hatching. The latter is contrary to Breed's findings. Mosley believes that learning, in the accepted sense, accounts primarily for increased accuracy in seizing objects, whereas striking and swallowing are more nearly unlearned responses.

Various interpretations have been put upon the work of Breed and those who have repeated his type of study. Some vary only in minute details, while others are diametrically opposed to the conclusions drawn by the authors. That is not at all surprising, however, for diverse interpretations of data usually obtain in research fields wherein it is difficult to bring all of the variables under experimental control. Bird is now repeating and extending his first investigations with the hope of ultimately obtaining a satisfactory solution of the controversy on the relative importance of maturation and use in the perfecting of the feeding responses of chicks. His report should soon be forthcoming in the periodical literature in the field.

Much of the early training of animals, and likewise that of preschool children, calls into use immature mechanisms for response, and, as is very well known, the efficiency of such training depends to some degree on whether the type sporadic investigations on animals have dealt with the maturational level of the child. As yet, however, only sporadic investigations on animals have dealt with the mental-age problem, but such as we have clearly indicate that different animals reach their maximal learning ability, or fractional parts thereof, at quite different ages in relation to their total life spans. Maximal learning ability in white rats for typical maze situations seems to be reached when they are from 1 to 3 months of age, or at a point in the rat's life span corresponding roughly to 3 or 4 years of age in children. In addition, one may say that apparently most of the higher animals attain intellectual and motor maturity very precociously as compared with man.⁽²⁵⁾ This fact renders especially difficult the task of obtaining inferential data for the genus *Homo* from comparative studies of the age factor in animal learning, an important point that lack of space forbids our giving further consideration.

Individual maturation is also dependent on habitual responses.—Although the newborn animal is equipped with certain unlearned responses by means of which he can satisfy the biological needs not taken care of by the parent, he quickly gives these unlearned responses specific direction and forms habitual responses that supplement those acquired through maturation. On the efficacy of the latter, to a great degree, depends the rate of subsequent maturational development. To illustrate, if young rats of weaning age are given a balanced diet in which cracked corn, oat flakes, or cracked wheat are constituents, it soon will be obvious that some litters leave untouched the cracked corn, some the oat flakes, and some the cracked wheat, whereas others eat the mixture as a whole. Only the latter grow at the optimal rate, and only the latter manifest their pubertal

sexual responses at the normal age. Eating habits of the discriminators have failed to supply them with all of the nutrients demanded for normal somatic and functional development. As may be inferred from the foregoing examples, those animals that form the more superior foraging and eating habits have in general the most accelerated post-natal development. To this the thought may be added that only those animals that supplement their unlearned defensive reactions by habits that efficiently protect them against specific animals of their habitats seeking them as prey, ever have the opportunity of perpetuating the species.

That some optimal amount of practice or use of an immature action system *per se* accelerates (never retards) the maturational rate is quite generally believed by trainers of animals and teachers of children. But, so far as the author knows, crucial data supporting this supposition have never been brought forward despite the fact that it is one of the most revered and widely voiced hypotheses to be found in genetic psychology. What seems equally plausible and more in line with scattered evidences is the hypothesis that maturational development is always primary and development by learning secondary in point of time and that these two types of development occur in relative amounts; that habits do not accelerate or retard maturational development except as they affect fundamental nutritional processes underlying somatic growth or maintenance; that at all times maturational development sets the upper limits for types and levels of habit formation, and that habits merely reflect or conceal, as the case may be, the maturational level reached. In subscribing to this latter statement, the author does not mean to minimize the value of habits as compared with unlearned responses, for in all of the higher animals, at least, both are indispensable. It is only by modification of the unlearned responses through use and as a result of success and failure that an organism adapts itself to the specific external environment in which it happens to begin

its independent existence and which it continues to use as a habitat; reorganization through practice or insight enables the immature and also the adult to meet specific requirements that only in equivalent form are presented to the species as a whole. In this sense, development by learning is both a supplement and an extension of maturational development.

Behavior That Is Called Instinctive or Innate

Unlearned responses manifested by young animals at birth, at definite stages of postnatal development, or in connection with periodically arising internal needs of the animal, usually go under the name of innate, native, congenital, or instinctive reactions. Examples of those appearing in the embryo, foetus, and newborn already have been cited in connection with our discussion of developmental schedules. Now attention should be directed to another type of unlearned responses, most typical of the adolescent and adult stages of life, which parallels less closely specific stages of somatic development than those heretofore discussed in connection with early stages of growth and differentiation. I refer specifically to the many types of defense reactions; movements of aggression in fighting; thermoregulatory behavior, involving particular postures, thigmotactic responses, or nest construction; hibernation and migration; reproductive behavior, including courtship, mating, protection of young, and ultimately dissemination of the family group; and the vast *ensemble* of nutritional responses involving selection of fluids, minerals, and other foodstuffs, and their acquisition, hoarding, and consumption. To make the list complete, of course one must canvass the total needs of the animal kingdom and assemble thousands of unlearned response mechanisms by which these needs are satisfied. But space limitations prevent our citing many specific examples to illustrate the relatively late-appearing

responses;* for the same reason, classifications are out of the question. That matters little, however, for examples and classifications are quite abundant in texts and periodical literature to which the student will have access.^(26, 27) But the student should not expect much help from the more formal classifications of instinctive functions. They are much too general and remote from the behavior data to serve his present needs. What he needs at present and what the experimental literature of this subject ultimately will supply in abundance is *very specific information on particular components of unlearned behavior in particular species of animals*. This information, insofar as it is complete, will pertain to such topics as the endogenous factors underlying unlearned responses, the motor mechanisms involved, the external stimuli or incentives toward which the activities are directed, the use of the exteroceptors in bringing organism and specific stimulus together, the neural organization of the mechanism, and so on.

As an illustration, we may cite the work on maternal behavior in vertebrates in order to indicate the types of problems experimentalists set for themselves in dealing with instinctive functions. The specific tasks are by no means identical if one essays to study maternal behavior in pigeons, domestic fowls, rabbits, guinea pigs, or rats, yet many of the general objectives have a great deal in common.

In the case of the rat, which has been more extensively studied than any other animal, the first problem was that of revealing the chief components of the maternal cluster.⁽²⁹⁾ They are parturition, cleansing of young, nest building and maintenance, nursing, defense, and retrieving. Then follow many types of researches that have as their aim: (1) description of the specific patterns of response

* Many of the data given in Chapter XIV are illustrative of the fundamentally instinctive responses which through experience have acquired special direction or restrictions that in some instances, at least, warrant our calling them *learned* or *habitual* responses.

involved in each type of activity; (2) determination of the rôle of specific external stimuli by which maternal behavior can be aroused; (3) determination of the endogenous factors that activate, prolong, and terminate the components of maternal behavior; (4) investigation of the rôle of receptors and localized areas of the cerebral cortex in maternal behavior, in comparison with other instinctive or learned responses of the more complex variety, and (5) determination of the conditions under which components of maternal drive are manifested in varying degrees of intensity. Most of the detailed facts on this subject can be found in a recent monograph by Wiesner and Sheard,⁽²⁹⁾ to which the reader now is referred for a continuation of the discussion.

Taking another example, one may say that the riddle of bird migration⁽²⁰⁾ has not yet been solved, but substantial progress toward its solution has been quite steady since the problem attracted the attention of experimentalists. Some of the more important steps consist of banding young and old birds to discover the *facts* of migration, i.e., time, course, and destination; charting of the diurnal and seasonal factors associated with movements of particular species or of several species occupying the same locality; comparisons of the "habits" of migratory and nonmigratory birds; analysis of the glands of internal secretion of wild birds sacrificed during each month of the year as well as of laboratory birds subjected to special experimental conditions roughly simulating the seasonal changes of temperature, amount of light and darkness, humidity, and so forth; experimental ablation of gonads in wild birds hatched in an incubator and subsequently allowed their freedom with the object of determining the effect of castration on the migratory impulse. In addition to the foregoing, there have been experiments in which old and young birds were taken from their nesting site and subsequently released at far-distant and unfamiliar places in order to determine their ability to

find their way back over great areas of open waters. Also, there are field and laboratory studies of the acuity of visual receptors; tests of learning ability and retention of habits in various species of fowls; and analysis of the neural mechanism associated with feeding and reproductive behavior of laboratory birds.

Similarly, we may say that no single theory can be invoked as yet to explain the hibernation of animals, but experimental studies are uncovering many important facts concerning hibernating animals.⁽¹⁹⁾ Researches have been chiefly addressed to the task of explaining (1) the tendency of certain animals to assume the temperature of the surrounding medium; (2) the absence of shivering and spontaneous movements; (3) the loss of consciousness; (4) the profound reduction in rate of metabolism; (5) the prolonged state of hypoglycemia without convulsions; (6) the cause for the subsequent awakening; and (7) the breeding activities almost immediately after leaving the hibernating state in some species of animals even though they are in a chronic state of inanition, when reproductive functions for many animals are at a low ebb. The relative ease with which laboratory conditions may be varied in order to determine the influence of thermal changes, food shortage, food abundance with resulting fatty deposits, particular glandular conditions, and so on, makes hibernation one of the favorite studies of instinct for the student of physiology. As yet, however, psychologists have not fully realized the possibilities of experimentation on this type of behavior.

In the chapter on motivation, which follows, we shall deal once more with the topic of biological needs and incentives to action, thus touching again upon certain aspects of the total problem of instinctive functions.

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CHAPTER IV

Motivation: Drives and Incentives

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Introduction

ANIMALS have more than one complex of internal and external stimuli playing upon them at a given time; hence, in experimental studies of motivation, one tacitly assumes that they are capable of reacting selectively and discriminatively to the various elements of their total environments. Let us see how readily this assumption can be supported by experimental evidence.

Consider Figure 5, which represents a laboratory room with a floor space approximately $10' \times 10'$. At the rear of the room is a home cage, *H*, and near the front are three inclined planes rising from the floor and extending toward the rear of the room. On the upper ends of the left and right inclines, respectively, are food and water. The center-most plane has only empty containers, which, in this experiment, serve to make the problem a bit more complex. White rats are allowed complete freedom of the room for about five days, after which they are shut up in the home cage for a period of 24 hours with *either* food or water in the cage, but never with both at once. After 24 hours, they are released, one at a time, and a complete record of their activities is made in order to determine whether they select the water or food in accordance with the internal

need (thirst or hunger) created by the period of deprivation.

A few of the animals give equivocal first responses; but the majority, on the very first test, go to the appropriate inclined plane and quickly climb to the food or water, according to the dominant internal need. When this experiment has been verified by the use of many animals and when the latter have nearly always made correct responses, we are willing to draw an inference that carries us somewhat beyond the data collected and yet is amply supported

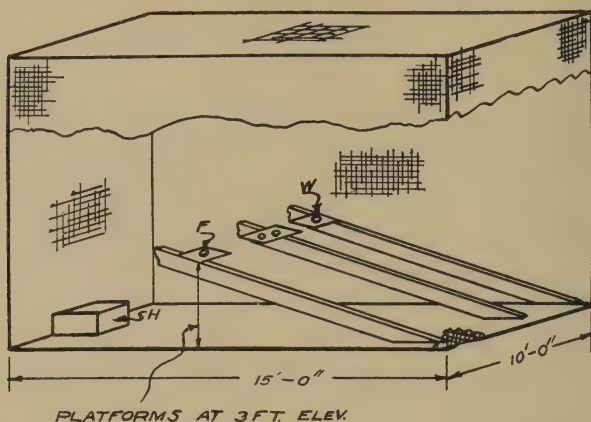


Fig. 5.—Floor plan of room in which differential responses to the internal states of hunger and thirst were tested. *H* is the release cage; *F* and *W* contain food and water.

by common experience. Henceforth we may tacitly assume that animals can and do select specific kinds of prey, seek others of their kind, and choose appropriate nesting sites and materials—in short, that they can and do discriminate between stimuli or objects by which their fundamental physiological needs are allayed or mitigated.

With the foregoing simple experiment as a background, we now have a satisfactory basis for defining three concepts with which we shall have to deal in the present chapter.

The term *motivation*, in its most typical sense, is used in animal psychology to denote a complex of dynamic factors by which an organism is aroused to perform specific reactions toward stimuli or objects of its environment. The external stimuli and the physiological states that serve to excite and, in a measure, to control the direction and persistence of responses are known, respectively, as (1) *incentives*, and (2) *internal needs* (i.e., *appetites* and *aversions*).

The term *drive* is more appropriately used to denote aroused tendencies in animals to respond to objects of their external environments that, in some measure, satisfy or alleviate a dominant physiological need. It is in the latter sense that we shall use the term.

Ontogenetic Aspects of Motivation

Biological needs of the immature go considerably beyond those of the adult because the tissues of the immature, in addition to clamoring for maintenance, must be differentiated and their cells produced in mass as organogenesis and growth get under way. From the beginning of individual life, aggregates of cells, activated and regulated by internal controls, help themselves to nutrients in the fluid medium about them according to the kind and amount of their specific requirements, just as newborn and adult animals take nutrients from their external environments according to specific tastes and hunger rhythms. At one time the site of greatest demand may be in the head region, at another the mid-section, and, still later, the lower extremities. These incessant demands are met both *timely* and *adequately*. To make this possible, a vascular system develops and expands just when a rapid and flexible transporting system is required; distant tissues and organs are integrated and automatically controlled by neural mechanisms that mature very early; glands of internal secretion become functional just as their products are needed to stimulate

and to regulate each other, as well as many other phases of organic development and maintenance; and finally, complex action systems involving the skeletal muscles become serviceable at the approach of each important physiological epoch, such as birth, weaning, dissemination of the family group, and sexual maturity—in short, just before any radical change in the organism's mode of living takes place.

Although such facts as we have just been considering may seem to pertain primarily to the province of physiology, they lie most certainly in a borderline field that the animal psychologist cannot afford to neglect. All of the unlearned responses are merely extensions of this early, more or less automatically developed system of physiological mechanisms by which the fundamental needs of an organism are supplied.

For purely methodological reasons, psychologists heretofore have centered their attention on problems of motivation as they arise in the more advanced stages of ontogenetic development. But now it is becoming more and more obvious that certain advantages may be gained if they endeavor to imbed the pillars of their subject in the prenatal (or equivalent) stages of life. By so doing, they may, for instance, be able to close an unwanted gap between motivation as it occurs in the prenatal and the postnatal course of development.

Experimental Studies of the Fundamental Drives

Studies of animal motivation have always been conducted through the medium of animal response. If one is particularly interested in the internal states that prepare animals to respond with specific action systems, he may plan his experiment so as to hold constant the external stimuli or incentives or so as to vary them only according to a predetermined schedule; and, conversely, if it is the mechanics of action or the incentives in which his interest

centers, he may allow the physiological state to vary no more than absolutely necessary or only according to a pre-arranged plan. Thus, conclusions that describe motivation in terms of responses to internal needs on the one hand and in terms of responses to incentives on the other may be reached despite the fact that *there is always an interlocking relationship among needs, action systems, and external stimuli or incentives.*

In the present section we shall be concerned primarily with physiological states or needs, and in the next, with activating stimuli; but, in either case, aroused action tendencies or responses will provide the numerical data from which conclusions are to be drawn. Were it possible here to deal comprehensively with theories of motivation, we should be interested in developing a universal organizing principle to which each classificatory heading of experimental studies would be logically related as the tailored glove is fitted to the hand; but since we are confronted with the problem of brevity, we shall merely assemble our illustrative studies under a few simple captions, each emphasizing a slightly different point in methodology or data-gathering.

The "present or absent" method.—This method is used to ascertain whether an overt response associated with a biological need does or does not appear upon presentation of its adequate stimulus in a standardized experimental situation. Its use generally implies that a threshold of internal pressure must be passed before a specific response mechanism is evocable by the standard adequate stimulus.

As a special illustration of the method, let us consider sexual motivation in pubescent rats as determined by their initial copulatory act. Previous experiments with adults⁽²⁴⁾ had revealed the proper incentive and the pattern of the reproductive response, hence the experimenter needed only to adapt his method to the special requirements of the younger animals.

As we have shown in other reports, the initial copulatory response is of the saltatory type and relatively complete in its first manifestations. It cannot be evoked by the normal incentive, however, until the animal has reached certain stages of maturational development in which the testes are liberating a considerable amount of internal secretion.

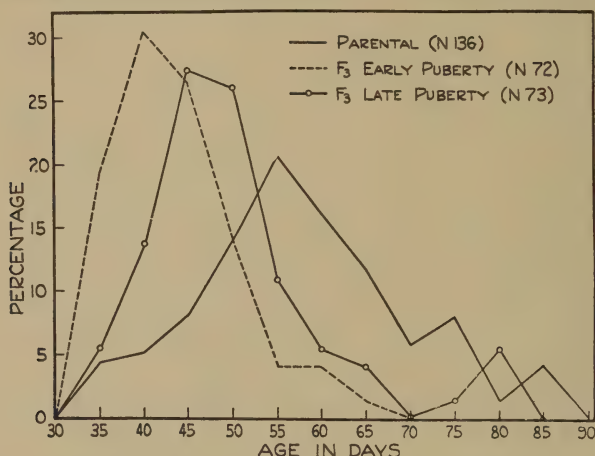


Fig. 6.—Age at sexual maturity of male albino rats as measured by the initial copulatory test. The solid line shows parental generation; dotted line, F_3 males produced by breeding early pubescent parental stock; dash and circle, F_3 males produced by breeding late pubescent stock. Selective breeding produced the differential between the F_3 groups. Improved testing technique is probably responsible for the mean of the late pubescent F_3 falling below that of the parental generation.

After many hours of testing, we obtained the data given in Figure 6. Unselected males provide the background against which two selectively bred groups are projected. As the controls clearly show, the age at which the copulatory act makes its first appearance is subject to wide normal variation, even in relatively homogeneous, inbred rats that are similarly housed, fed, and tested. The graph at the left of this figure is a distribution of F_3 males produced by interbreeding successive generations of males and females

having early puberty. On the right of the figure is a similar distribution of F_3 males obtained by interbreeding successive generations of late pubescent parents. No factors, except the ages of puberty of the parents, were varied to produce the divergent results obtained from the two F_3 groups. Therefore we may assume that the differences are due primarily to genetic factors as expressed in the ontogenetic development of the young. Thus, it becomes apparent that the initial manifestation of this specific drive reflects maturational development of the immature, and this fact, in turn, reflects a particular genetic constitution.

Extensive studies similar to the foregoing have been made by Slonaker⁽²¹⁾ on the climacteric in senescent female rats; by Stone on the waning of copulatory drive in rats and rabbits following castration^(26, 27) and also on the effects of inanition on the age of first reproductive responses⁽²⁵⁾; by Avery,⁽¹⁾ who investigated homosexual behavior in guinea pigs; by Hulbe and Stone⁽¹¹⁾ and by Wiesner and Sheard⁽³⁴⁾ on the maternal drive in parturient and virgin rats; and by many others who at the time were not interested in the more quantitative aspects of motivation in relation to variable internal states or types of incentives.

From the foregoing examples, we may infer that the method of "present or absent" may be very useful in determining whether animals are sufficiently mature to exhibit particular responses, such as tropistic movements, reflexes, and so forth; whether an internal state is of sufficient strength to activate one of the well-known responses like sucking, drinking, scratching, fighting, fleeing, and so forth; or whether a specific incentive arouses positive, negative, or some other orientational response. Also, it may be useful in preliminary test situations wherein the experimenter wishes merely to know whether his animal has the *Aufgabe*, the set—in short, is ready for a more elaborate or quantitative test. The method can hardly be put to quan-

titative use except when the experimenter has ranked his criteria of internal need or incentive appeal so as to form a graded scale. If the latter has been done, he may check these indicators as to presence or absence and thus obtain a rough measure of the strength of the underlying metabolic need or incentive appeal. Carpenter,⁽³⁾ for instance, thinks that preening of feathers, billing, and overt copulatory responses in pigeons are ranked in the same order as are the degrees of internal sexual pressure respectively required to arouse them. Studies on savageness and wildness in rats⁽²⁸⁾ also indicate that certain types of responses are characteristic of only the wildest of the wild; others, of the moderately wild; and still others, of those possessing only the milder degrees of this temperamental trait.

Frequency of response in a standard test-interval.—The least equivocal of all methods of measuring the strength of drive is that of direct enumeration of repetitive responses made in a relatively short observation period and functionally associated with a particular physiological need. As we shall see, it is well adapted to quantitative work with many modalities of response.

(1) *Complete copulatory acts.*—As a first example of the method, let us consider the data of Table III, columns 1 and 2, in which is given the frequency of complete copulatory acts by adult male rats tested individually at the approximate age of six months. The males were reared on a well-balanced diet and were allowed to eat *ad libitum* from the age of weaning. All of them were thoroughly cage-adapted and accustomed to performing the reproductive act under similar conditions. During the month preceding the tests proper, they were separated from females; but just two or three days prior thereto each male was allowed two or three minutes of cohabitation with a receptive female in order to acquaint him thoroughly with the test situation. Four tests were made. The first two came on the same day, and the second two, one week

later. Each test was of 15 minutes' duration and an interval of 20 minutes was interspersed between tests 1 and 2 and between tests 3 and 4. It will be seen that the frequency of complete copulatory responses ranges from 0 to 55 for the half-hour tests. The averages for the first and

TABLE III

FREQUENCY OF COPULATIONS BY MALE ALBINO RATS
APPROXIMATELY 6 MONTHS OF AGE

Rats noted in columns 1 and 2 were tested in two 15-minute periods with a 20-minute rest period between; the data of columns 1 and 2 were gathered one week apart on the same individuals. The data of column 3 were collected during 1 hour of uninterrupted testing; those of columns 4 and 5 were gathered in a 2-hour period of uninterrupted testing. All animals of columns 1-3 were of the Slonaker stock, Stanford University, and reared in the psychological laboratory; those of the last two columns were of the Wistar stock, and tested in the Columbia University laboratory of psychology. The specific test situation was similar in all cases.

Frequency	N=33		N=16	N=27	N=79
	$\frac{1}{2}$ hour (Stone)	$\frac{1}{2}$ hour	1 hour (Stone)	2 hours (Nissen) ⁽³²⁾	2 hours (Jenkins) ⁽³²⁾
0	1	1	0	15	58
1-5	0	0	0	0	1
6-10	2	2	0	0	3
11-15	2	5	0	0	3
16-20	2	1	0	0	2
21-25	7	10	0	1	1
26-30	7	6	0	0	4
31-35	5	4	1	0	0
36-40	4	0	1	0	0
41-45	1	2	0	1	0
46-50	0	2	1	2	2
51-55	2	0	3	1	2
56-60	0	0	3	1	1
61-65	0	0	2	1	0
66-70	0	0	0	2	0
71-75	0	0	2	2	0
76-80	0	0	1	0	0
81-85	0	0	0	1	0
86-90	0	0	0	0	1
91-95	0	0	1	0	1
96-100	0	0	1	0	0
Mean for those copulating	29	26	62	59	32

second half-hours are 28.8 ± 2.5 and 25.6 ± 2.3 , and the S. D. of the distributions are 11.9 ± 1.8 and 10.7 ± 1.6 .

By definition, a copulatory response is a unitary sexual act; hence its frequency may be taken as a *valid* indicator of drive. From the available data, it is possible also to ascertain the reliability of copulatory scores by correlating the data obtained from the two half-hour tests. The Pearsonian correlation for the first and second half-hours is $.74 \pm .05$. The reliability coefficients for these data may be increased by applying a legitimate correction to the raw data. It is well known that many males, after approximately 5 to 10 copulatory responses, deliver a special discharge (plug), after which they are inactive for several minutes. Although the frequency with which these discharges appear is an indication of the virility of the animal, the period of complete idleness materially reduces the frequency of copulatory responses. Therefore, credit should be given for each of these discharges. Certain statistical calculations indicated that an addition of 10 points to the copulatory score for each special discharge would be the most efficient change in correcting the reliability coefficients derived from raw scores. By so doing, the r for the half-hour tests is raised to $.84 \pm .03$. Applying the Brown-Spearman formula to the data in order to obtain the reliability for the one-hour test, the coefficient .91 is obtained. In the light of these coefficients, we may conclude that, under the conditions of this experiment, a fairly reliable measure of copulatory drive is obtained.

The necessity of careful standardization of direct tests of drive is indicated when one attempts to compare results obtained in an experiment such as the foregoing from different laboratories. In columns 5 and 6 of Table III are given copulation scores reported by Nissen ^(33:282) and Jenkins ^(33:192) for male rats of the Wistar stock that were tested for two consecutive hours. Data

obtained by the author in a one-hour test by a method of testing that is believed to be essentially like that of these investigators are given in column 4. Had the author's test extended through a second hour, the differences in scores obtained would have been greatly increased, for his animals were quite active at the end of the first hour. What, we may ask, caused this great discrepancy? The final answer cannot be given; but we surmise that the difference has arisen from different habits established in the males, different conditions of nutrition, unrecognized variations in experimental technique, slight differences in the genetic strains of the rats, or any one of several other possible factors. Obviously, *comparable measures of any drive can be obtained only when conditions are well standardized.*

(2) *The obstruction method.*—Of the many instrumental devices employed to measure and to contrast the strengths of drives, none has been more highly standardized or extensively used than that of the obstruction method of Warden⁽³³⁾ and his co-workers at Columbia University. The method appears to be a logical descendant of several previous investigations, the most important forerunner being that of Moss.⁽¹⁴⁾

An animal, placed in one compartment of the apparatus illustrated in Figure 7, may reach the incentive in a near-by

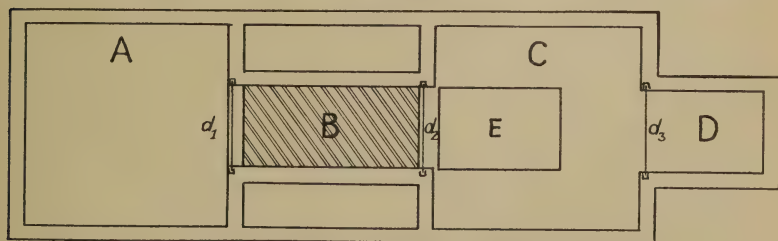


Fig. 7.—Floor plan of the Columbia University obstruction box. A, entrance compartment; B, obstruction compartment or grill; C and D, divided incentive compartment; E, release plate; d_1 , manually operated door of entrance compartment; d_2 , automatic door (operated by release plate) between two divisions of incentive compartment.⁽³³⁾

compartment by crossing an electric grill from which it receives a mild shock. The number of approaches to the grill, contacts, and crossings are taken by these workers to indicate the strength of drive under the conditions of the experiment. So flexible is their general program that, with minor adaptations, different animals, as well as a variety of biological needs, may be studied comparatively.

(a) *Validation*.—In making the obstruction method meaningful for studies of internal motivation, the investigators were obliged to demonstrate, in each instance of its application, that crossing the grill was a valid indicator of the presence as well as the strength of the dominant physiological state. This they did by showing that animals crossed the grill when an incentive was present but that crossings were relatively rare (1) in the absence of the physiological state, (2) when there was satiation with respect to the incentive, or (3) when the incentive chamber was empty.

The following data from a study of the female sex drive in rats ^(33:161) will illustrate the kind of evidence on which validation of this method rests. The experimenter wished to test females in various stages of the oestrous cycle. Hence all animals, except those known from the application of inspectional methods to be in heat, were selected at random and then classified by subsequent microscopic examination of the vaginal smears, permanently mounted for study and comparison. The different stages of oestrus represented, the number of cases employed, and the results from the twenty-minute test in terms of crossing, approaching, and contacting the grill are given in Table IV. Differences between crossings by each of the groups are statistically significant. Furthermore, there is little doubt that they were responding to the presence of the male, because they crossed significantly oftener than receptive females tested without the male incentive. Using this apparatus with male rats, the same author demonstrated that

it was a valid measure of masculine sexual drive. In the Stanford laboratory, the latter point has been verified once more: our experiments show that any male that copulates in the home cage will copulate almost immediately upon reaching the incentive chamber. Frequency of copulation in the home cage is also positively and significantly correlated with frequency of crossing the grill.

TABLE IV

RESULTS OF (1) A SEXUALLY RECEPTIVE FEMALE GROUP WITH MALE INCENTIVE, (2) A RECEPTIVE GROUP WITHOUT ANY INCENTIVE, AND (3) A NON-RECEPTIVE GROUP WITH A MALE INCENTIVE. After Warner,⁽³³⁾ Table 12, page 161.

N.	Classification	Crossings		Contacts		Approaches	
		Mean	σ	Mean	σ	Mean	σ
21	Cornified (receptive)	14.61	5.14	3.14	2.73	5.43	3.63
22	Cornified (controls, no male)	5.05	2.55	2.27	1.91	3.23	2.7
32	Dicestrus (nonreceptive)	1.34	1.57	1.47	1.27	1.16	1.42

(b) *Reliability*.—Warden and Nissen^(33:34) undertook to answer the following question with respect to reliability of scores: "Do the individual indices obtained in an initial test hold their relative positions in later retests under the same general conditions?" They used a retest method on eight rats with hunger operating as the internal motivating factor, and from the experiment drew the following conclusion: "So far as the evidence goes, the method seems to have a relatively high self-correlation, although such a conclusion should finally rest upon a larger body of data." In the Stanford laboratory, a second test of reliability has been made. The adult male rats whose reproductive scores are given in Table III, columns 1 and 2, were tested in the Warden obstruction apparatus on two occasions approximately seven days apart. We recorded the number of contacts with the grill and the number of crossings made by each animal during a twenty-minute interval. Since contacts and crossings appeared to be the

complement of each other, these scores were thrown together. The correlation of the combined scores for tests 1 and 2 is $.84 \pm .03$. From this result, we may conclude that with adult male rats, the obstruction apparatus yields fairly reliable scores on sex drive. It is doubtful, however, whether one should say that reliability as determined under one specific condition of motivation gives an adequate basis for inferring reliability under radically different conditions.

(c) *Recovery of sex drive in male rats following satiation.*—Figure 8 graphically illustrates the average

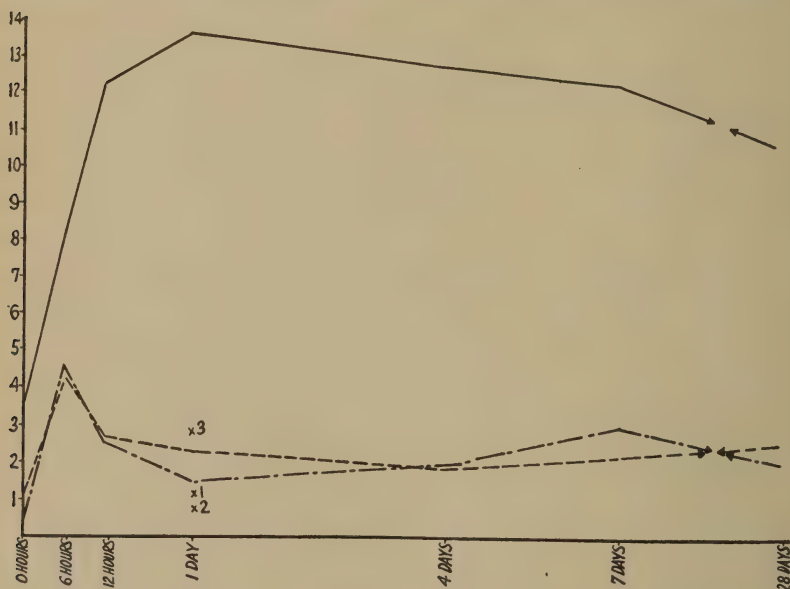


Fig. 8.—Male sex drive for different intervals after copulatory “satiation,” as determined by the obstruction method. The average number of crossings is shown by the solid line; the contacts, by the dot-and-dash line; the approaches, by the line of dashes. The results for controls, which had no female incentive, are shown on the one-day abscissa because they were tested only after a 24-hour deprivation period; for the controls, the numbers 1, 2, and 3 refer to the average number of approaches, contacts, and crossings. There were 20 animals in each group and each animal was given one 20-minute test. (After Warner, Fig. 9, page 154.⁽³²⁾)

number of approaches, contacts, and crossings of the electric grill by 160 males tested after various hours of deprivation following the two-hour copulation period. Table V gives

TABLE V

NUMBER OF INSTANCES OF CROSSING, CONTACTING, AND APPROACHING AN ELECTRICALLY CHARGED GRILL BY GROUPS OF RATS HAVING VARIOUS PERIODS OF ABSTINENCE FROM COPULATORY ACTIVITY FOLLOWING A 2-HOUR SATIATION PERIOD OF COPULATION. The controls worked without incentive. Each group has 20 cases. Twenty-minute tests. After Warner, ⁽³³⁾ Table 5, page 151.

Group	Crossings		Contacts		Approaches	
	Mean	σ	Mean	σ	Mean	σ
Control	2.95	1.8	1.05	1.18	1.2	1.03
0	3.6	4.08	0.35	0.7	1.2	1.36
6 hours	8.1	5.2	4.5	2.77	4.15	3.26
12 hours	12.2	4.8	2.65	1.98	2.7	2.03
1 day	13.45	4.03	1.5	1.5	2.3	2.35
4 days	12.6	6.24	1.85	1.56	1.8	1.9
7 days	12.25	7.07	3.1	2.5	2.25	1.5
28 days	10.55	7.1	2.0	1.97	2.5	2.9

the average and the standard deviations for approaches, contacts, and crossings. In Table VI are given the data that denote the significance of differences between crossings for the various temporal intervals. From a consideration of the data of these tables it may be seen that the animals that have just had a two-hour period for copulation are no more willing to cross the grill than a control group, which had no incentive object beyond the grill. Six hours of abstinence, however, brings about a significant difference in the number of crossings. Twelve hours is likewise better than six, and very much better than zero. The intervals of one day, four days, one week, and four weeks give significantly more crossings than the zero interval, and as a general rule are better than six hours; but no significant differences for the intervals beyond six hours are obtained, although the figures for the twelve-hour interval and the

one-day interval approach significance in comparison with the four-week interval. The 28-day interval yielded a somewhat smaller mean than the twelve-hour, the one-day, and so on, yet the difference is so small that one may surmise that uncontrolled factors *other than sexual drive* may have been responsible for them.

TABLE VI

SHOWING RELIABILITY OF THE DIFFERENCE BETWEEN THE AVERAGE NUMBER OF CROSSINGS OF THE MALE GROUPS OF TABLE V
After Warner,⁽³³⁾ Table 6, page 151.

Group	Difference	Diff. ÷ S.D. Diff.	Chances in 100 of a True Difference Greater Than 0
0 hours and 6 hours	4.5	3.06	100.0
6 hours and 12 hours	4.1	2.59	99.5
12 hours and 1 day	1.25	0.89	81.0
1 day and 4 days	0.85	0.51	69.0
4 days and 7 days	0.5	0.24	60.0
7 days and 28 days	1.55	0.69	76.0
1 day and 28 days	2.9	1.6	94.0
1 day and control	10.50	9.2	100.0

This experiment reveals in the rat a rather rapid recovery from a single period of sexual satiation. An interesting extension of the study would be that of testing for the cumulative effect of satiations. Such an experiment would correspond more exactly to life situations in which one essays to determine the effects of excessive indulgence, as in the experiments of Slonaker.⁽²²⁾

The scores denoting normal female drive at different stages of the œstrual cycle have already been given in Table IV. It may be noted that the highest score for crossings by males and the highest for females are not significantly different. Without further samplings of animal groups, however, and complete control of the early histories of the male and female subjects, little warrant for generalizing as to sex similarity or sex difference in drives can be

given. Males of the Stanford laboratory copulate two or three times more frequently and cross the grill much oftener than those reported by the workers at Columbia University. As yet, however, no corresponding rise for female scores has been obtained.

(d) *Effects of gonadectomy, vasotomy, and injections of gonadal extracts.*—Nissen ^(33:262) obtained very similar amounts of crossing of the electric grill, when a male incentive was used, by normal females in heat, pseudo-castrates in heat, and castrates that had received injections of the ovarian hormone. In marked contrast with these three groups stand the females that were in the diœstrum and likewise the castrates that received no injections of the ovarian hormone. Neither would have copulated and likewise neither crossed the grill to reach the male more than two or three times, on the average. Experiments with the male castrates, though less conclusive than those with female castrates, suggest that the obstruction technique is adequate to distinguish between the sexual drive of normal males, castrates of one month, and castrates of three or more months. Concerning the results of orchitic injections and vasotomy, little of a positive and conclusive nature can be given from the experiments so far reported, but we may expect positive results with further experiments of this type. Only recently have reliable testicular extracts been prepared.

Space limitations prohibit our doing more than calling attention to the very interesting studies of Jenkins ^(33:179) on social factors and habituation, which may influence male and female drive, and on maternal drive, as reported by Nissen; ⁽³³⁾ but in leaving this subject we may say that the excellent studies already performed and the interpretative setting in which they have been placed by Warden ⁽³³⁾ cause us to hope that obstruction methods will be put to many additional uses in comparative studies of animal drives. The revival of this method by Moss ⁽¹⁴⁾ and its sub-

sequent standardization by the Columbia University laboratory deserve to stand as important landmarks in the evolution of experimental techniques for the study of animal drives.

(3) *Materials used in nesting.*—Using the drum pictured in Figure 9, upper right, Kinder⁽¹²⁾ studied heat-regulatory behavior in rats. When strips of paper are hung over the

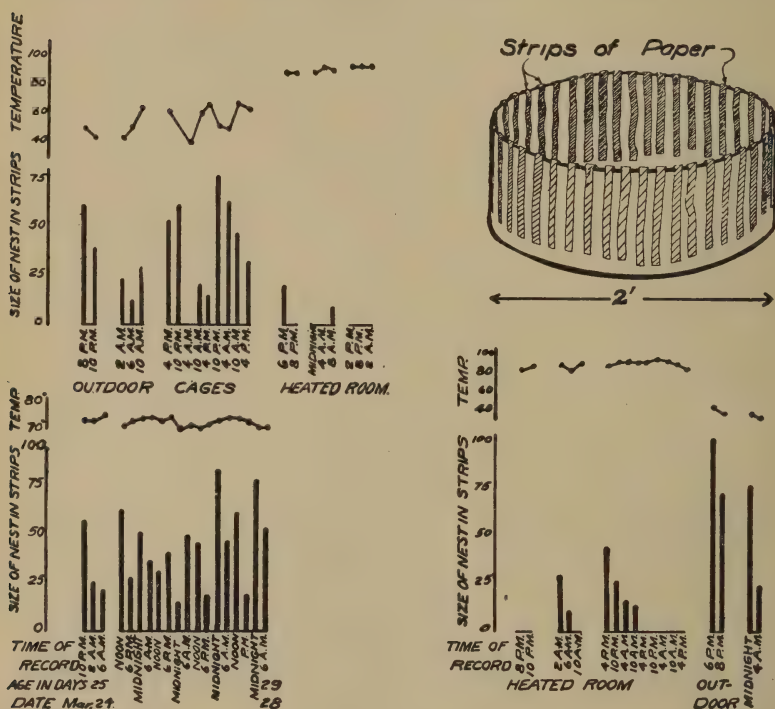


Fig. 9.—Showing strength of nest-building drive in rats. In the upper right-hand corner is an open drum over which narrow strips of elastic paper are hung; a rat enclosed in the drum can pull down the paper and use it for nest construction. The column diagrams give a quantitative representation of strength of the nest-building drive, as indicated by the number of strips of paper used under the varying conditions of temperature. (After Kinder.⁽¹²⁾)

edges of this drum, the rat gathers them in to construct a nest. The number of strips pulled in gives a quantitative measure of nest-building activity in relation to thermal needs or other physiological states, particularly those of post-parturient females. Although the reliability of scores was not reported by Kinder and has never been determined by other workers, her published data clearly show a high degree of consistency from day to day. Hence, in all probability, quite reliable scores are yielded by the method when all conditions of the experiment are carefully standardized.

Figure 9 illustrates some of the results obtained by Kinder. In the upper left-hand corner is shown the activity of a young female 28 days of age that was housed for 70 hours in an outdoor cage, followed by 34 hours in a heated room. Outdoor and indoor temperature variations are indicated at the top of the figure. Columns 1 and 2 show the amount of nest building in 2-hour periods; the next 3 columns, that in 4-hour periods; and the next 9, in 6-hour periods. The same order of observations is followed when the animal is in the heated room. In each test, 140 strips of paper were offered and at the end of each observational period all used material was removed. In the lower right-hand corner of Figure 9 will be found results for a litter mate of this same animal. Her first records were taken for 70 hours in a superheated room and with observational periods duplicating those of her sister in the outdoor cage. Following this is her outdoor record for 12 hours. In the lower left-hand corner of the figure we have nesting activity by a control animal kept in isolation under conditions of normal room temperature. Her activity is intermediate between that of animals housed in the superheated room and that of those in the outdoor cage. On the whole, the method nicely reveals temporal and quantitative relationships between thermal need and heat-regulatory behavior.

Kinder finds little difference between the average amount of nesting by males and females of similar ages, but in the case of the adult female, there is periodicity, which is associated with her œstrual cycles. While in the receptive phase of œstrum, she does little nest construction as compared with the amount done during the diœstrum. A great amount of nesting is associated with parturition and subsequent activity until the œstrual cycles begin again.

The activity cage: a measure of spontaneous behavior.— Various kinds of activity cages have been devised ⁽¹⁷⁾ to measure the amount of spontaneous activity of small animals. They are so mounted that the animal's movements activate a counting device or a lever arm in contact with a continuous kymograph drum. Of these various instruments, the revolving cage is the most widely used. Validity of its scores rests chiefly on temporal coincidence of the peak of activity and the greatest internal need (water, food, heat, and so forth) created by fasting or deprivation. The reliability of scores may be determined by correlating data from repeat tests or data from odd and even days in a limited observation period. ⁽¹⁷⁾ A simple example will reveal the chief virtues of this apparatus as a measure of drive.

If an adult female rat is put into a revolving cage that is provided with an automatic revolution counter, the daily activity record obtained will be about like that illustrated in Figure 10A, in which the frequency of revolutions is indicated on the ordinate and successive days of the experiment on the abscissa. The numbers on the graph indicate successive days in which the number of revolutions start at a low point and mount upward, the peak of activity corresponding to the time at which the female is in œstrus. Figure 10B shows the burst of activity coming at puberty. Figure 11 illustrates various correlated factors in the reproductive cycle. At the top of the figure, cage activity is indicated on each of 5 successive days; next, the time of

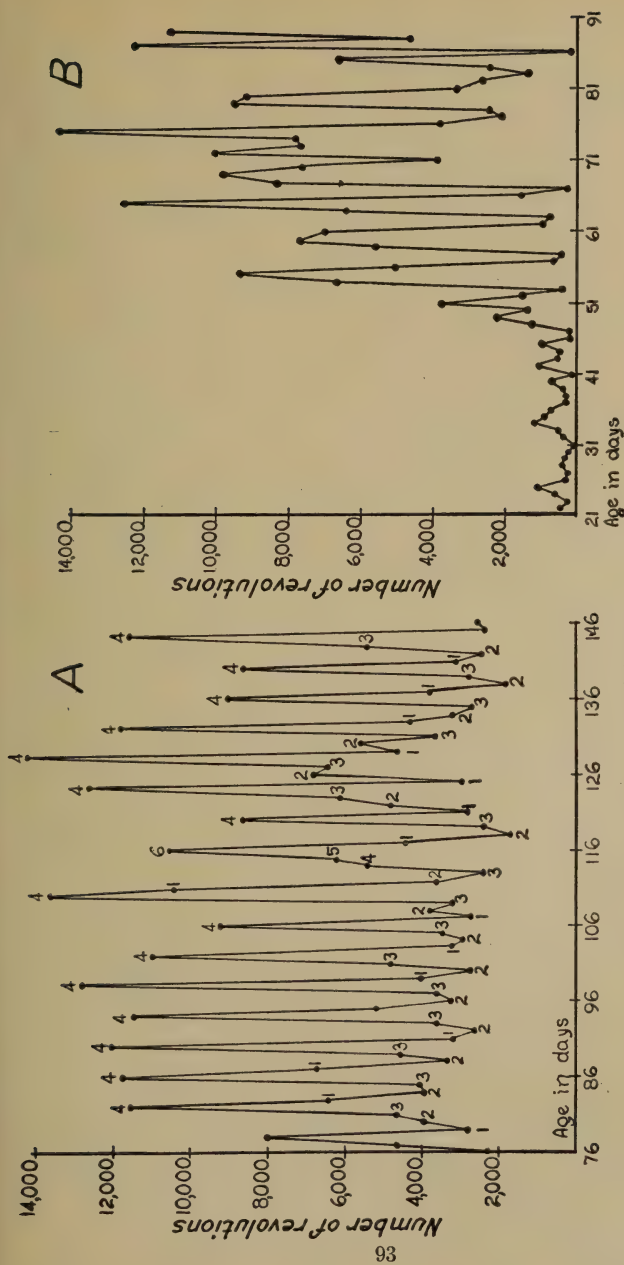


Fig. 10

At left (A).—Revolving drum record of a normal female rat, showing the cycles of excessive running, corresponding to estrual cycles. (After Richter.⁽¹⁵⁾)

At right (B).—Revolving drum record of young female rat, showing the onset of cycles of excessive activity at the age of puberty. (After Wang.⁽²²⁾)

sexual receptivity is indicated; and below is given the cell picture of the reproductive tract, which undergoes a course of changes associated with œstrus. Nucleated epithelial cells appear just before cornified cells, and the latter are associated with receptivity and the greatest activity.

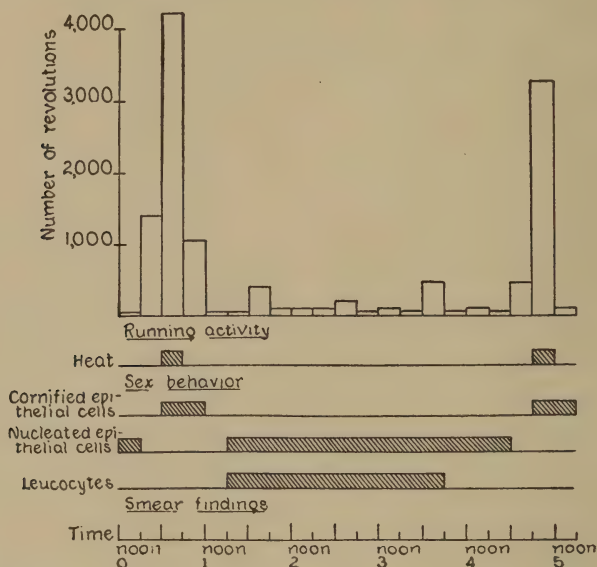


Fig. 11.—Temporal relations between running activity, sexual receptivity, and the ovulation cycles established for six-hour records. The rat was 130 to 135 days of age. (After Wang.⁽³²⁾)

In this method of studying sexual drive, each animal is a self-control, and strength of drive on one day is contrasted with that on another. But to make a comparative study of sexual drive with such variables as age, stages of pregnancy, lactation, nutritional level, vitamin deficiency, drugs, social facilitation, and so forth, would not be difficult.

Although Richter⁽¹⁵⁾ has suggested that the more virile male rats are likewise the more active in the revolving drum, our own extensive test of this point yielded negative

results. The males whose data for copulatory responses are given in Table III, columns 1 and 2, were allowed 5 weeks of cage activity. The first week was discarded inasmuch as the animals required that amount of time to become thoroughly familiar with the revolving drum. Using the total revolutions for 4 weeks, we have correlated these data with frequency of copulatory acts and found zero correlation. Likewise, these scores were correlated against scores obtained from the Warden obstruction apparatus, but again the coefficient was in the neighborhood of zero. Since the direct test and likewise the obstruction apparatus give valid and reliable measures of sexual drive, we may assume that the data from the revolving drum probably are not valid measures of sexual drive in males.

For many other applications of the activity method, consult the review by Shirley.⁽¹⁷⁾

The satiation method.—This method is a variation, or better, an extension of the frequency of response method. One begins with a dominant drive operating under standard conditions, and, without varying the external stimuli or incentives, continues the experiment until no further actions are called out by the incentive. The indicators of strength of drive will be, of course, such records as the total number of responses, the total time interval during which actions are called out, and the slope of the curve denoting frequency of response per unit of time.

As an example of this method we may briefly consider the illuminating work of Bayer,⁽²⁾ who shows that hunger alone does not determine the volume of food consumed by hens, but that many variations in the external environment which are surprisingly independent of the state of hunger have an effect on the matter. Bayer finds that hens allowed to eat to their full satisfaction, then not fed for 24 hours, and again allowed to eat individually from a pile of 100 grams of grain until satisfied, will eat from 33 to 35 grams more when confronted with a larger heap; hens that have eaten

spontaneously until satisfied will eat again repeatedly when the remainder of the pile is quickly removed with a brush and immediately returned, many hens eating as much as 67 per cent more; hens required to pick up the grain by pecking on a hard surface will eat approximately 40 grams, but if allowed to eat from a soft surface, they will eat approximately twice as much, the difference being due to the difference in painfulness created by the hard surface against which the bill is struck; hens will eat approximately two or three times as much whole grain as of cracked grain; and a hen that has eaten to complete satisfaction in isolation will again begin to eat when another hungry hen is placed before the heap of grain, sometimes eating 60 per cent additional food because of the social stimulus. This amount is still further increased if three instead of two hens are introduced; but conversely, if three hens are allowed to eat until satisfied and subsequently a single hen is introduced, the three hens pay no further attention to the food. The three hens apparently form a unity of behavior that is not susceptible to the influence of the isolated hen. Experiments of this kind have great possibilities for the study of social facilitation of animal drives and should be applied to many drives other than hunger.

Skinner ⁽²⁰⁾ has opened up another interesting aspect of the satiation problem and in this connection has made one of the most important contributions to methodology so far reported. His basic assumption is that the amount of food eaten per unit of time is proportional to the strength of the metabolic needs that are activating the eating reflexes. A cleverly adapted mechanical device allowed his rats to obtain uniform pieces (20 pieces per gram) of a homogeneous food mixture and at the same time made a record on a kymograph drum each time a piece of food was taken. His records show that the frequency with which the rat visits the food supply diminishes in an orderly manner until there is total cessation. The records are similar to curves for a

power function $N=Ktn$, in which N is the amount of food eaten at a time t , K is a constant for a given experimental situation, but varying from situation to situation, and n is another constant with a narrow range of variability (0.67 to 0.71) for all of the experimental settings. Although the full possibilities of this method have not yet been worked out, any student with a bit of imagination will readily see that literally dozens of important applications of the method are possible. In addition to varying the deprivation interval, such things as palatability of food, the age of the animal, sex, competing drives, social facilitation, and so forth, should be investigated. With slight alterations of method in which drops of water are substituted for pellets of food, no doubt thirst can be studied in a very effective manner.

In the Stanford laboratory, preliminary experiments on sex behavior in male rats have been undertaken for the purpose of bringing out some of the more striking psychological factors affecting the renewal of sexual activity in rats after satiation. So far, the introduction of new females is the most effective factor in re-activating males that have already ceased to copulate, but many other factors, as well, have a similar though less potent influence.

Counterbalance or contrast of competitive drives.—This method is founded upon the “present or absent” and the frequency of response methods, but differs in having at the same time two or more biological needs aroused and in presenting appropriate incentives for each, thereby requiring the animal to choose between the alternatives. Direction of choice indicates prepotency of one internal state and its appropriate action over the other internal state and its appropriate response. Many variations of the foregoing method are to be found in the literature on the subject; some variations place emphasis on the internal state, and others, upon the external incentive. The latter are sometimes designated as preferential or choice methods.⁽³⁵⁾

The tendency of wild and timid rats to hide rather than to come into the presence of the experimenter to obtain food when hungry illustrates the counterbalance of motives method. The simple apparatus pictured in Figure 12 was used. Rats had the alternative of hiding and thus making themselves inaccessible to the experimenter or of coming around to the open cage for food. If the animal did not come into the food box within 10 minutes, it was credited with a failure for that day and was deprived of food. No food was given during the 48-hour interval prior to the first test; thus hunger was very keen.

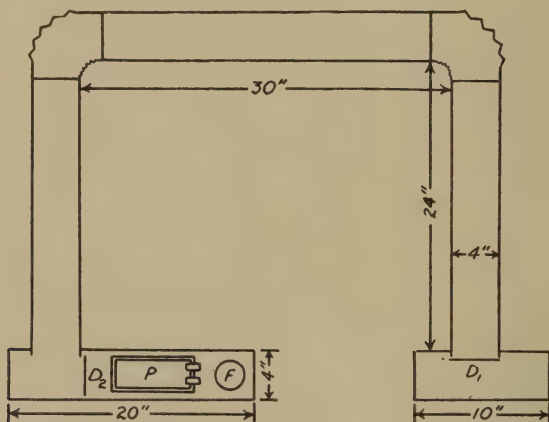


Fig. 12.—Concealment apparatus. D_1 and D_2 are doors that prevent retracing. P is a platform upon which the animal steps in passing to F , the food cup. The platform P , when depressed, sounds a buzzer which informs the experimenter that the animal has reached the food box: then D_2 is dropped. The tubes are made of black stovepipe.

Results from three groups of rats similar as to caging, feeding, and handling prior to the age of 100 days, but different as to genetic constitutions, will be considered. Group 1 is composed of 25 typical domesticated albinos; Group 2 is composed of 28 half-breeds obtained by crossing

albino females with wild brown males; and Group 3 is composed of 10 full-blood wild males. Figure 13 graphically illustrates the percentage of each group that came into the food box within the first minute of the test given on 10 successive days. On the right side of Figure 13 will be found

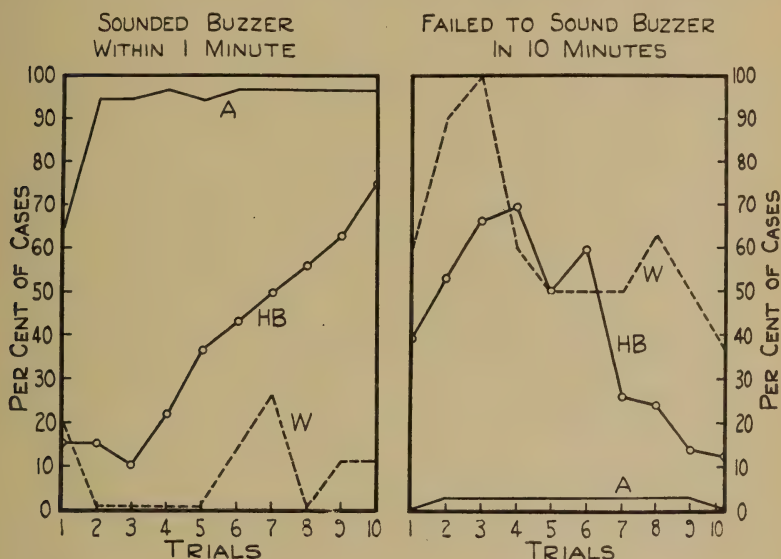


Fig. 13.—Results of the concealment tests. On the left is shown the percentage of animals completing the circuit to obtain food within one minute; on the right is the percentage that remained hidden in the tube for the entire period of 10 minutes. A, albinos; HB, half-breeds; W, wild stock.

the percentage failing in 10 minutes. It will be seen that the wild and half-breeds stand in striking contrast to the albinos. A few of them came around with great hesitation during the first minute of the test, but the majority avoided coming out to the experimenter. In the case of many of the half-breeds and wilds, not ordinary hunger but acute

and prolonged inanition was required to overcome their hiding tendency.

In this experiment one may readily see that two conflicting drives are present in the total experimental situation and that the animal is unable to act according to these two kinds of internal states at the same time. However, in the course of the experiment one observes that the hunger seems to acquire dominance over fear. Further study by this same method shows, however, that when the appetite for food is partly satiated, the fear again becomes dominant. When animals are timid and wild, an internal state such as hunger which is built up during 2 days of food deprivation can be subordinated to the fear complex within two or three minutes. On the other hand, several weeks may be required to dispose of the fear complex in favor of hunger by taming the animals.

The preferential or choice method is illustrated by an experiment of Tsai, ⁽³¹⁾ who attempted to determine the relative strengths of the sex and food drives. Tsai concluded that the hunger drive was stronger than the sex drive, but a suspended judgment of the legitimacy of this conclusion may well be held until the experiment has been repeated. Tsai did not use males that in direct copulatory tests showed the presence of sexual drive. This point, of course, negates any fundamental generalization from the experiment.

A well controlled series of experiments that reveals the many possibilities of the choice method and that at the same time may be taken as a model in scientific method is that of Young, ^(35, 36, 37, 38) who worked on the relative food preferences of rats. Although space does not allow us to present his data, we may say that the student who reads this series from beginning to end will be amply repaid for his time.¹

¹ For additional details, see Chapter VII.

The Effectiveness of Incentives in Learning Situations

During the past decade an increasing number of experiments that deal primarily with the effectiveness of incentives have been performed. These studies are usually grouped together in studies of animal drives and designated as the "learning" method. Since the point of emphasis seems to be on the incentive, however, we have felt justified in giving them greater emphasis by setting them off from the other studies of drive.

Studies of incentives in learning situations.—(1) *Appropriateness and reward value.*—Using a fourteen-unit maze, Elliott ⁽⁶⁾ trained a group of 25 hungry animals to run the maze for the reward of a moist, mixed diet that had excellent qualities for maintenance and growth; the diet is a very palatable diet as well. At the end of 10 trials, when the group was making an average of only $1\frac{1}{2}$ errors per trial, the experimenter changed the reward to sunflower seeds, and at the same time gave only sunflower seeds in the home cage to supplement that eaten at the end of the trials. As will be seen from a consideration of Figure 14A, the error curve immediately rises. In other words, the rats did not perform according to their knowledge of the maze. This continued for the following 6 days, after which another regime was inaugurated by the experimenter. At the end of the 16th trial, he split the group into subgroups. To one of these, Group B, he restored the original incentive of mixed diet and to the other, Group A, he continued to give the sunflower seed but took away all supplementary seeds in order to insure a much stronger degree of hunger motivation. The groups responded to the change in incentive on the one hand and to the increased hunger motivation on the other. From this experiment it must be obvious that both the incentive and the degree of internal drive, want, striving, or whatever one may choose to call it, play an im-

portant role in the performance of rats on the maze problem.

Still further exemplifications of the principle that the drive must be suited to the incentive offered and that the incentive must also be appropriate to the drive are brought out by Elliott ⁽⁷⁾ in another experiment. Three groups of rats were trained to go through a 14-unit multiple-T maze ²

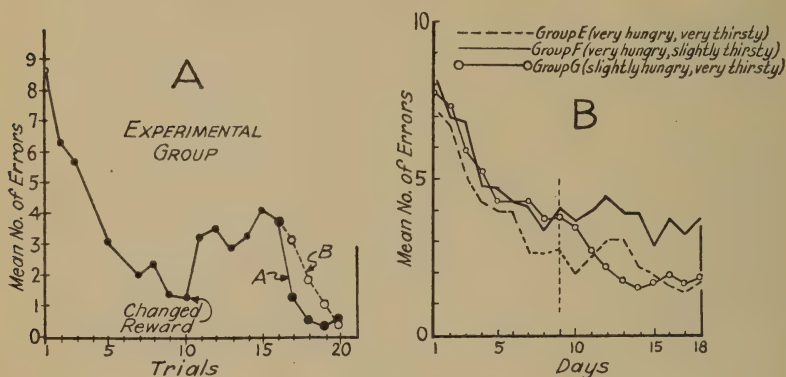


Fig. 14

At left (A).—Effect of change of reward. (After Elliott,⁽⁶⁾ Fig. 1.)

At right (B).—Effects of appropriateness of reward and of complex incentives on maze performance. (After Elliott,⁽⁷⁾ Fig. 1.)

with food in the form of a moistened mash as the incentive for the first 9 days and with water as the incentive for the next 9 days. Group *E* was very hungry and very thirsty each day; Group *F* was very hungry and only slightly thirsty; and Group *G* was slightly hungry and very thirsty. Obviously, the food might be expected to appeal differently to these groups because of the varied internal drives in operation at the time of the trials; similarly, the water appealed differently to the three groups and in a manner that might be expected to differentiate their responses from those elicited by the food reward. The error

² Illustrated in Chapter XI.

curves for these groups are given in Figure 14B. The group that was very hungry and very thirsty did somewhat better than either of the other groups on the first 9 trials, but it appears to have balked soon after the water alone was introduced; a decided improvement followed the introduction of water in the case of Group *G*, which was only slightly hungry but very thirsty. Group *F*, on the other hand, balked almost completely after the 9th trial. It was very hungry but only slightly thirsty in this case. The deprivation of food and offering of water did not incite the animals to run the maze better than at the end of the 9th trial, although a continuous drop was to have been expected if the incentive had been appropriate.

(2) *Quantity of reward*.—In a preliminary trial series, received between the ages of 5 and 10 days, 70 chicks were trained by Grindley ⁽⁹⁾ to run down a 4-foot passageway to obtain food. In these trials, grain was scattered at various places in the runway and the animals were required to look for it as they made their way toward the farther end. Next, each animal was allowed 4 trials to find a grain of rice placed in a certain position in the passageway. On the basis of these trials, the fifty "best" chicks were selected and divided into five groups of ten each. In the actual experiment, a reward was placed out of the chick's sight at the extreme end of the runway. Group 1 received no rice at the end of the run; Group 2 received one grain of rice; Group 3, two grains; Group 4, four grains; and Group 5, six grains. One trial per day was given on seven consecutive days.

The score for each chick is 100 times the reciprocal of the time in seconds required for it to go from the release box to the food tray. From these scores, means for the five groups were computed and the results plotted as in Figure 15A. One may observe that the animals receiving no reward made almost no progress in running quickly to the food tray. On the other hand, those that received the

greatest amount of food have the best record, and in each case the record varies according to the amount of food received. Thus, it is apparent that the performance of the chicks in this experiment reflects in a rather consistent and direct manner the reward value of the runs to the food tray. In continuation of this work with chickens, a second experiment with an important variation was performed. In the latter situation, the food was not visible during the

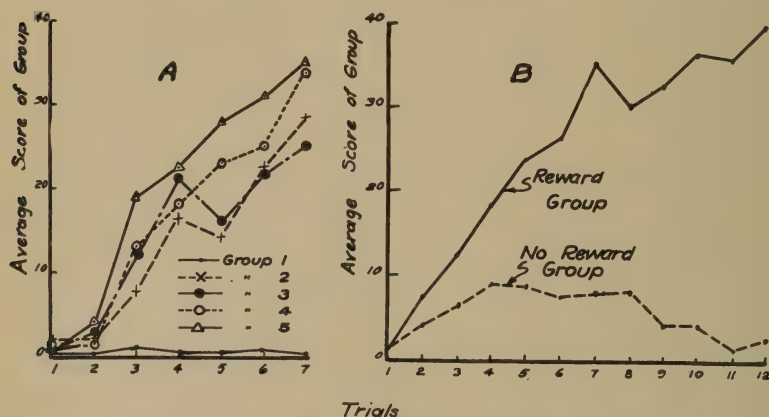


Fig. 15.—The Effects of Different Quantities of Reward on the Learning Rate of Chicks. (After Grindley,⁽⁹⁾ curves 1 and 2a.)

course of the run. In this, as in the first experiment, the chickens that received the reward immediately set up the habit of rushing out to the food box, whereas the others did not form such a habit at all. The time records are shown in Figure 15B. Obviously, there is a close relationship between reward and level of performance.

(3) *Degrees of hunger, reward, and non-reward.*—In a striking manner the experiments of Tolman and Honzik⁽³⁰⁾ show the relationship between degrees of hunger and reward, and non-reward, and the maze performances of rats. The experiment is somewhat like that of Grindley, which

has been described above, but in this case rats instead of chicks were studied. A 14-unit T-maze was used and 4 groups made up of 36 individuals each were trained. The animals were given similar preliminary training and during this time were similarly motivated. Then the experi-

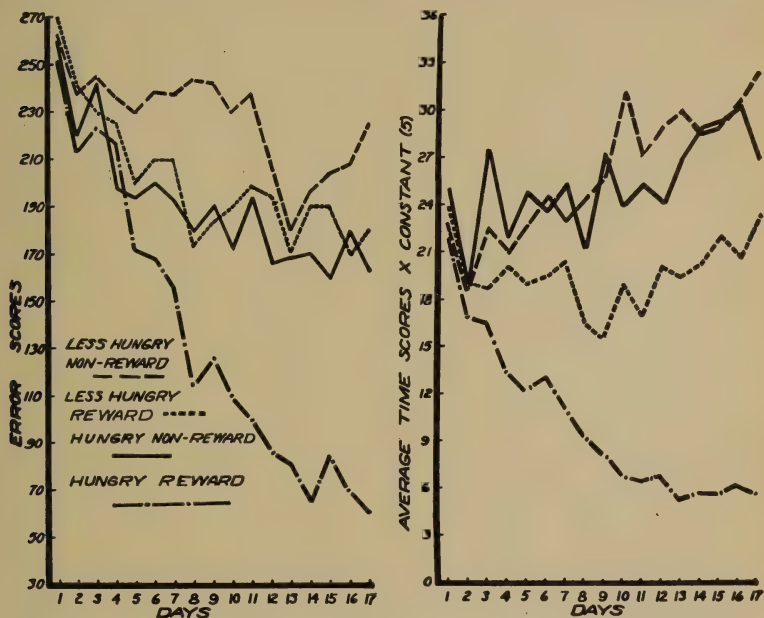


Fig. 16.—Error and time curves for four groups of rats trained on the maze with varying degrees of hunger and with reward and non-reward. (After Tolman and Honzik.⁽³⁰⁾)

ment proper was carried out with the groups in various states of hunger and receiving various amounts of food reward. One hungry group received its full ration at the end of the daily run; another hungry group did not receive any food at the end of the trial; a third group was only slightly hungry and received a full ration; and a fourth was slightly hungry and received no reward. Without going into the complete details of the experiment, we may say that the results are as indicated in Figure 16 so far as the error and

time scores are concerned. These curves, self-explanatory in nature, show clearly that there is a striking correlation between performance on the one hand and the interrelationship between internal drive and reward on the other.

Comparative efficiency of stimuli or incentives.—The old problem of punishment versus reward as incentives to learning crops up from time to time. As heretofore, the results obtained from recent experiments vary with the intensity of the punishment, its effectiveness, and its meaningfulness to the animal, as well as with the nature, quantity, and appropriateness of the reward. Likewise, several experiments have been performed with a relatively constant internal state and a relatively constant task to be performed but with variable kinds of rewards offered. These experiments show a measurable relationship between performance and the amount or quality of the incentive used. Somewhat different from the latter experiments are those in which the task to be performed is constant but the internal state and the reward as well are varied. Perhaps the recent experiments of Ruch ⁽¹⁶⁾³ on the relative effectiveness of food and escape from water as incentives to maze learning best illustrate this type of study. So closely tied up with the more general studies of learning are experiments of the foregoing kind that we shall refrain from dealing with them more explicitly in this connection. For an extensive and critical review of this work, however, the reader will be richly rewarded by turning to such reviews and discussions as those of Simmons, ⁽¹⁹⁾ Ligon, ⁽¹³⁾ Warden, ⁽³³⁾ Tolman, ⁽²⁹⁾ and Diserens and Vaughn. ⁽⁵⁾

Augmentation and Diminution of Drives and Incentive Values

Normal variations in the strength of drives have been noted for homogeneous groups of animals by every investi-

³ See Chapter X for additional details.

gator who has employed reliable quantitative measures. The more comprehensive studies also indicate that strength of drives or incentive values varies greatly by way of either augmentation or diminution with variations in such general factors as age, sex, health, available organic and inorganic foods, water, heat, disturbances of endocrine balance, toxic conditions produced by drugs, presence or absence of young, social factors to which the animals give attention, and previous experience with stimuli that are likely to arouse pain—in short, all those conditions that may cause appreciable variations in the physiological states or needs, the mechanisms of response, or the incentives to action.

As a specific example, we may say that spontaneous activity in animals confined in the revolving drum, particularly such rodents as the rat or mouse, is augmented by acute inanition, thirst, temperatures falling below the optimal range for a resting animal, darkness, nicotine and sodium phosphate, rests interspersed between prolonged periods of activity, presence of other active rodents, abstinence from sexual activity of the female leading to pregnancy, or brain lesions of the frontal lobes. Depression of activity may result from chronic malnutrition extending over a long period of time or from the final stages of inanition leading to starvation or dehydration, from prolonged dosing with alcohol or caffeine, from excessive fatigue induced by forced activity, from gestation and lactation, from removal of the gonads or the anterior lobe of the hypophysis, from very gross lesions of the cerebral cortex, and from many factors that call out fear or hiding responses.

Without doubt, one can find factors that will change the strength of any drive whatever. Therefore, it is not unreasonable to demand of experimenters that they give a fairly complete statement of all details that may throw light upon the motivation of animals used in a given experimental situation. This demand is applicable not only

to studies of learning, insight, retention, and so forth, but also to studies of the unlearned responses.

Perversions and Other Abnormal Manifestations of Drive

There are certain manifestations of drive in which the actions of the animal are directed to an atypical stimulus or incentive; these commonly go under the general name of perversions of instinctive activities, or perversions of appetites. Green ⁽⁸⁾ has reported several interesting perversions of appetites for food in domestic animals. Sheep that were fed a ration consisting of maize endosperm and a minimal ration of autoclaved hay (a diet faulty in both mineral and vitamin content) developed the wool-eating habit and nibbled at each other continually when brought into the yard. Cattle deprived of phosphorous spend much of their grazing time searching for bones. When there is only a mild condition of mineral shortage, the cattle eat only the clean dry bones; but when it is more acute, they will eat green bones to which putrefying flesh is still adhering. Young cattle brought up on a phosphorous-deficient soil from which bone *débris* has been completely removed will manifest the bone-eating tendency the first time bones are displayed before them in the feeding troughs. A liberal ration of phosphorous compounds leads to rapid disappearance of the perverted appetite in most cases and prevents its appearance in young animals. The habit quickly returns, however, if the ration is temporarily withheld.

In this connection we may mention the perverted sexual responses of adult animals that are deprived of opportunity of cohabitation with animals of the opposite sex. ⁽¹⁰⁾ Either excessive indulgence, deprivation, or even social habituation may change in striking manner the incentive values of many patterns of stimuli or incentive objects.

A Generalized Program for Future Investigations of Motivation

The advanced students who find complete satisfaction only in going behind the curtains of methodology and concepts in order to come to grips with processes themselves, in animal behavior, may find the loosely organized materials of the preceding pages inadequate to satisfy their highly laudable interest in the subject of motivation. Such students are already prepared to deal directly with the sources of this subject, either in the capacity of critical readers or in the capacity of experimenters, and require no further consideration. However, the student who is now making his first acquaintance with the experimental literature of motivation may profit by further consideration of a generalized program for research in this field.

Let us note once again that experimental studies of motivation are always conducted through the medium of animal responses. These responses are regarded as indicators of the presence of a physiological condition or state that is momentarily dominant. They are directed, as a rule, toward some object or stimulus pattern of the external environment that has an *interlocking* relationship with the physiological state and when avoided or possessed by the organism satisfies, alleviates, dissipates, or otherwise alters this dominant physiological state. The common goal of experimental studies is delineation of characteristic modes of response, defining their direction with respect to objects or stimuli of the external world, measuring the vigor of action as indicated by duration and frequency of response, or by work done in a given interval of time, and, finally, defining the dominant physiological states or needs that are fundamental to the actions and that in the last analysis are the *sine qua non* of motivation.

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CHAPTER V

The Effect of Drugs and Internal Secretions on Animal Behavior

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Deprive the brain of oxygen for a few seconds and consciousness is gone; remove the thyroid gland and a beautiful and intelligent child becomes a hideous imbecile; subject the egg-cell of some species to an appropriate salt-solution and an individual will develop without a father. The absence of certain chemical bodies prepared inside the body by the thyroid gland, the lack of oxygen to carry on the necessary combustions in the brain cells—both simple chemical changes—have obliterated the essential characteristics of the highest form of life. Wherever we look we find life in only one form, composed of compounds of hydrogen, nitrogen, oxygen and carbon, living between certain narrow limits of temperature, giving out exactly as much as it takes in, dependent upon the supply of foodstuffs from outside, exhibiting certain electrical properties, poisoned and destroyed by the most absurdly small doses of certain chemical substances. ⁽¹¹⁾

Importance of Internal Chemistry in Behavior

THERE is no important aspect of the behavior of living organisms that cannot be markedly influenced by chemicals. The most excruciating pain may be abolished by morphine, and the most restless state may be subdued with some of the chemical derivatives of barbituric acid that quiet the nervous system and produce sleep. Even the deepest and longest sleep known in the animal world—the hibernation of the bear or hedgehog—may be effectively terminated by the proper injection of an extract from the

thyroid gland. The imbibing of too much alcohol not only disturbs motor control and coördination but produces even more profound effects on the so-called higher mental processes. Life itself is probably nothing more than a series of progressive chemical changes. The frequent reports presented in the daily press of individuals that are "brought back to life" by the injection of adrenalin into the heart muscle demonstrate the supreme importance of internal chemistry in the human machine. In short, all that we are and do is actually the result of the coördination of innumerable chemical forces, including the very humblest.

Since the time of the most ancient medicine man, the human race has been looking for certain drugs and chemicals with which to fight the many ills that flesh is heir to. Various concoctions of herbs, inorganic materials, and preparations from animal bodies were tried in a blind trial-and-error search for means of ridding the body of disease and of restoring internal peace and happiness. It is only within the last few decades that this search for efficacious drugs has been at all scientific. The change to a much more scientific method of determining the potency of drugs has been brought about by animal experimentation. The common saying "try it out on the dog" typifies this modern point of view in pharmacology. Some of the most powerful drugs in the pharmacopœia are standardized on such laboratory animals as the rat, guinea pig, frog, dog, and rooster. Diphtheria antitoxin, for example, is standardized on the guinea pig. Many of the glandular products, such as the sex-stimulating theelin, are standardized in terms of "rat units." Digitalis, the heart stimulant, is standardized in terms of its action on excised frog's heart, and the potency of ergot is measured by its action on the combs of roosters. The reason for the use of this "biological assay" method is the fact that there is so much similarity between the physiological effect of these drugs in the lower animals and in man.

Drugs other than endocrines.—In this section will be considered very briefly some experimental work to determine the effect on animal behavior of a few of the more important drugs. Many other drugs could be discussed and many more experiments could be given with the few drugs discussed herein, but these will serve as fairly typical illustrations of the enormous work done in comparative psychology that carries over directly into the fields of pharmacology and psychiatry.

(1). *Opiates.*—As far back as recorded history goes, men have used the poppy to relieve their pains and to give relief from the toils and monotony of existence. No other chemical so far discovered by man will so quickly make him oblivious to the trials and tribulations of this world and indifferent to the uncertainties of the next. The price paid for the continued use of this substance is invariably hopeless addiction, accompanied by degeneracy and mental disease. The immense psychological effect of opium is brilliantly described in the following passage from De Quincey's *Confessions of an English Opium-Eater*:

I took it; and in an hour, oh! Heavens! What a revulsion! What an upheaving, from its lowest depths, of the inner spirit! What an apocalypse of the world within me! That my pains had vanished was now a trifle in my eyes;—this negative effect was swallowed up in the immensity of those positive effects which had opened before me—in the abyss of divine enjoyment thus suddenly revealed. Here was a panacea for all human woes; here was the secret of happiness, about which philosophers had disputed for so many ages, at once discovered; happiness might now be bought for a penny and carried in the waistcoat pocket; portable ecstasies might be corked up in a pint bottle; and peace of mind could be sent down by mail.

There is unfortunately a less bright side to the very enthusiastic report of De Quincey, namely, confirmed addiction, leading to complete mental and physical chaos. In the final stages, the individual shows marked muscular weakness which may become so extreme that standing is difficult. A sense of crushing fatigue comes over him; con-

traction of cutaneous blood vessels produces a feeling of cold; interference with digestive activities leads to gastrointestinal upsets, accompanied by vomiting and diarrhoea and followed by a most obstinate constipation. In the mental realm are found restlessness and inability to concentrate. Extreme depression and misery follow the withdrawal of the drug. Suffering is increased by the persistent insomnia.

During recent years, the theory has been developed that drug addicts are suffering from some complex or some emotional thwarting and use the drug as a "means of escape from reality." Those who adhere to this theory believe that addiction is purely a mental, rather than a physical, condition, and that the only way to cure the drug addict is to work on his mind rather than his body. To put this theory to a test, a series of very carefully controlled experiments were conducted by Kolb and DuMez, ⁽¹⁴⁾ investigators in the United States Public Health Service, using monkeys as the test animals. In these experiments, they tried the effects of three opiates, morphine, codein, and heroin, to determine the degree of tolerance, if any, that could be acquired, and also to determine whether the administration of these drugs over comparatively long periods of time would cause the animals to become dependent upon them to maintain the equilibrium of certain bodily functions.

The authors' summary regarding addiction to the drugs is as follows:

By daily administration of morphin, heroin, and codein, monkeys were made tolerant of increasingly large doses. After 8 or 9 months, 200 milligrams per day of morphin caused less severe immediate symptoms than 10 to 40 milligrams did during the first six weeks; 39 milligrams of heroin caused less severe symptoms than did 4 milligrams at first; and 110 milligrams of codein caused less severe symptoms than did 10 milligrams in the beginning. One animal that was started on morphin was kept on it or on heroin for 52 months.

Gradual deterioration in general health was caused by daily adminis-

tration of codein, morphin, and heroin. Codein was decidedly the most harmful, and heroin the least.

Codein caused convulsions frequently, heroin much less often, and morphin never. ⁽¹⁴⁾

Among the most interesting findings of these investigators were those in regard to withdrawal symptoms. The marked withdrawal symptoms in these animals when the drug was omitted after dependence had been built up would seem to strike quite a blow at the theory that withdrawal symptoms in human beings are simply hysterical "baby-with-its-rattle-taken-away" reactions, capable of being controlled by the will of the patient. We could hardly so consider these symptoms in the experimental animals. The following section is quoted from the report of Kolb and DuMez: ⁽¹⁴⁾

Withdrawal Symptoms.—During the latter part of June, 1923, it was observed that the animals were more restless on Monday mornings than on other mornings, but there was no definite evidence of discomfort. The animals began to receive two daily doses on June 26, but the Saturday afternoon doses were omitted during the summer. During the latter part of July, four months after the injections had been started, definite withdrawal symptoms were observed in all animals following the 48-hour period of abstinence. They were hypersensitive to noise and more resistant to handling. Some had occasional slight twitching of the muscles, and all showed the peculiar grin indicative of discomfort. The symptoms disappeared in from 15 to 20 minutes after the dose of morphin had been given.

Withdrawal symptoms gradually became more evident. By the end of September, some of the animals would be found doubled up with apparent abdominal discomfort on Monday mornings. About this time, withdrawal symptoms were evident in some of them every morning due to the 17 hours of abstinence following the last dose given at 4 p. m. the day before. Beginning on October 28, one injection was given on Sundays in order to avoid the debilitating effect of repeated withdrawals. The animals were then receiving daily doses of 180, 180, 160, 180, 180, and 170 milligrams respectively.

The depressing effect of withdrawal was most strikingly illustrated in No. 6; abrupt withdrawal was attempted when this animal was receiving 190 milligrams of morphin daily. It had been on the drug for 9½ months and was showing considerable evidence of hypersensitivity and discomfort every morning until the morphin was given. The last dose (95 milligrams) was injected on the morning of January 13. The animal was then in good condition. The usual evidence of hyper-

sensitiveness and discomfort occurred during the next few days, but the most striking effect was the depression of vital functions as shown by the fall in temperature, which is given in Table VII.

TABLE VII

TEMPERATURE RECORD OF No. 6 DURING WITHDRAWAL OF MORPHIN

<i>Date</i>	<i>Temperature at</i>	<i>Dose of Morphin</i>
1924	9 a. m. (°C)	
Jan. 13	38.0	96 milligrams
Jan. 14	37.6	None
Jan. 15	36.0	Do.
Jan. 16	36.6	Do.
Jan. 17	36.2	Do.
Jan. 18	34.1	Do.
Jan. 19	32.0	25 milligrams (9 a. m.)
Do.	32.0	50 milligrams (3:30 p. m.)

The morphin was given on the 19th in an effort to save the animal, but it had no apparent effect, death occurring at 8 p. m. The necropsy showed beginning pneumonic process in the right lower lobe. In this case depression of vital functions rendered the animal susceptible to pneumonia, and it is of interest to note that there was no capacity for reaction with fever.

For the facial expression and attitudes resulting from the discomfort of withdrawal and the comfort following injection of the usual dose, see Figures 17 and 18. The animals were photographed immediately before the morning injection of morphine was given and from 15 to 30 minutes following the injection.

(2). *Barbituric acid derivatives*. Barbital (veronal) is a hypnotic substance widely used as a relatively safe sleep-producing drug. It is prescribed by physicians in such conditions as nervous insomnia and certain types of mania and delirium. A moderate dose induces a deep, dreamless sleep in half an hour or less. The drug is excreted slowly, so that continued use tends to be cumulative in the effect of the drug. There are many instances of veronal addiction, and restriction of its sale is recommended because of this tendency.

In a well-controlled experiment, Omwake ⁽¹⁶⁾ attempted

to determine the influence of barbital on the activity and learning of white rats, hoping in this way to throw some light upon its effect on human beings. In the experimental group were 94 rats, each of which received an intraperitoneal injection of 100 mg. per kilogram of body weight of 1-per-cent solution of sodium salt of barbital on alternate days for four and one-half months. A control group of 73 rats of the same age received identical food and care and were given the same tests but no barbital.

A maze served as the device for measuring activity and learning. Trials were always made between 48 and 72 hours after the last injection of barbital to insure that the animals would not be under the immediate influence of the drug. The index of activity was the number of errors made per minute while the rat was in the maze searching for the reward, since a rat if active would either make errors or proceed immediately to the reward box. The measure of learning was the percentage of rats locating the reward within a specified time. Tables VIII and IX summarize the results.

When the activity of the barbital rats is compared with the activity of the control group, it is evident that the bar-

TABLE VIII

ACTIVITY OF WHITE RATS UNDER THE INFLUENCE OF BARBITAL
MEASURED BY ERRORS PER MINUTE

<i>Group</i>	<i>Number of Errors per Minute</i>			<i>Number of cases</i>
	Q_1	<i>Median</i>	Q_3	
Barbital	1.5	2.5	3.9	94
Control	1.6	3.0	4.4	73

TABLE IX

TIME REQUIRED TO FIND THE REWARD, BY WHITE RATS
UNDER THE INFLUENCE OF BARBITAL

<i>Group</i>	<i>Number of Minutes per Trial</i>			<i>Number of cases</i>
	Q_1	<i>Median</i>	Q_3	
Barbital	3.4	7.7	16.5	53
Control	2.4	4.7	9.6	66



Fig. 17.—Effects of Drug Addiction

Upper.—Monkey No. 5, at end of 25-hour period without the drug.

Lower.—On same day, 30 minutes after injection of 100 mg. of morphine sulphate.



Fig. 18.—Effects of Drug Addiction

Upper.—Monkey No. 6, at end of 25-hour period without the drug.

Lower.—On same day, 30 minutes after injection of 95 mg. of morphine sulphate. (From *Public Health Reports*, No. 1463.)

bital group was consistently less active than the control group of the same age.

The number of minutes required to find the reward was considerably greater for the barbital group.

A study of the effect of barbital on the sex and maternal drives of the female white rat was made by Wilcox.⁽²²⁾ She injected 30 young female rats between seven and eight weeks old with barbital every 48 hours for nine months. Careful check was kept of the estrus cycle through the use of the vaginal smear method as described by Long and Evans,⁽¹⁵⁾ and from 48 to 72 hours before the next expected estrus period, the injections were discontinued, allowing sufficient time to be sure that the animal was not under the immediate influence of the drug. The strength of the sex drive was measured by the Moss obstruction method—measuring the number of times the female would approach, contact, and cross charged electric plates to get to the male. All those tested were in estrus, but the rats injected with barbital showed markedly weaker sex drive than non-injected females of the control group. Table X gives a comparison in averages of the sex drive of non-injected and injected females.

TABLE X

STRENGTH OF THE SEX DRIVE IN WHITE RATS UNDER THE INFLUENCE
OF BARBITAL

<i>Groups</i>	<i>Av. No. of Approaches</i>	<i>Av. No. of Contacts</i>	<i>Av. No. of Crossings</i>	<i>Av. No. of Volts</i>	<i>Time in Minutes</i>
Injected	17.4	14.4	8.5	44.8	11.5
Non-injected	19.5	19.3	18.7	98.5	4.4

This experiment shows that a normal rat will approach 2.1 more times, contact 4.9 more times, cross 10.2 times more frequently, and stand 53.7 more volts in 7.1 less minutes than a rat that has been injected with barbital for over a period of 9 months.

In the same study, the author reports a marked decrease in the fertility of the rats. Only 9 of the 30 that mated became pregnant, and of these 9, 5 gave birth to dead litters, 2 ate their litters as soon as they were born, and only 2 had normal litters.

(3) *Drugs influencing catatonia and allied conditions in animals.*—For years scientists have wondered about such peculiar states as catatonia, in which the limbs remain for hours or even days in a fixed position, even though the position be a most absurd and unnatural one. Patients suffering from such conditions are nearly always negativistic and refuse to answer questions or pay any attention whatever to their environment. Catatonia is frequently seen in one type of dementia præcox. The cause of this condition is still more or less of a mystery, but some animal experiments are beginning to throw considerable light upon it. It is beginning to appear that the state of catatonia is caused by the presence of certain toxic substances in the blood stream, and that it can be remedied by injecting other chemical compounds that act in an antagonistic way to these harmful substances.

Various investigators have found that a catatonic condition closely resembling that seen in man can be produced in animals by the injection of bulbocapnine. Soon after the injection of the drug, the animal goes into a typical catatonic state that lasts for varying lengths of time depending upon the dosage and other factors. Since it is known that this catatonic state can be produced by a drug, it is natural that drugs should be sought to correct it. The following is a summary of such an investigation:

Buchanan and Richter ⁽³⁾ experimented on 8 monkeys, giving them bulbocapnine in doses based upon the amount of 50 mg. for the adult animal. The injected monkey, with his extremities bound so that only one hand was free, was lifted by his head and his free hand brought into contact

with a horizontal bar. The animals under the influence of the drug would grasp the bar and hang freely by one hand for a considerable length of time. An animal that had not been injected would not hang at all. To the same monkeys, cocaine hydrochloride in doses of from 8 to 26 mg. (from 2 to 5 mg. per kilogram of body weight) was administered subcutaneously at various intervals before and after the injection of bulbocapnine. The experimenters report the following results:

1. Experimental catatonia produced by bulbocapnine in monkeys is eliminated by injections of cocaine. The animals behave normally almost at once and do not return to the stuporous condition.
2. Cocaine injected before bulbocapnine prevents the appearance of the catatonic syndrome.
3. The hanging response which appears in *Macacus rhesus* monkeys when they are under the influence of bulbocapnine is eliminated by cocaine. Objective records were thus obtained of the effect produced by cocaine on bulbocapnine catatonia.

Of course, no one would take the risk of throwing a normal person into a catatonic state by injecting bulbocapnine, but patients who are already in this condition as a result of such a disease as dementia præcox have been brought out of it by cocaine injections. Inasmuch as cocaine is a habit-forming drug, most investigators prefer to use some less dangerous drug to counteract the catatonic condition. The substance most commonly employed for this purpose is a high concentration of carbon dioxide.

Solomon, Kaufman, and D'Elseaux ⁽¹⁹⁾ have forced catatonic patients to breathe 40 per cent carbon dioxide and 60 per cent oxygen, and by so doing have been able to bring the patients back to a period of normal lucidity, accompanied by more or less spontaneous activity, which lasts, on the average, from 15 to 25 minutes. At the end of this period, a somewhat startled, amazed, and confused expression comes over the patient's face. He begins to move more slowly, responds to questions with difficulty, his an-

swers become delayed, and he shows inability to recall names that he was able to recall easily a few moments before. At the end of another ten or fifteen minutes, the original condition is regained. These investigations would indicate that catatonia is caused by a disturbance in the chemical environment of the nerve cells, and that it can be remedied by changing this environment.

The effect of endocrine secretions.—The ductless glands, or endocrines, exert their influences on animal behavior by pouring into the blood stream certain chemical substances called autocoids. These substances are carried by the blood to all parts of the body and are taken in by the tissues, whose function or structure is modified by them. The chemical nature of some of these substances is definitely known, and two of them, thyroxin and adrenalin, have been synthesized in the laboratory. Considering them as drugs, they are remarkably potent. For example, the secretion of the posterior lobe of the pituitary, which stimulates smooth muscles, produces maximum contraction in the muscle when the pituitary substance is diluted 1:15,000,000,000. The secretion from the adrenal medulla can be detected by biological tests in dilution of 1:200,000,000. Stating this another way, to reduce an ounce of adrenalin crystals to the above dilution would require the contents of 40 miles of water carts, each holding 325 gallons and placed 200 carts to the mile. The thyroid hormone is likewise so powerful that the average man has only about one-fourth of a grain in his body, but that amount makes the difference between imbecility and normality.

In this section a brief consideration will be given to the following glands: (1) thyroid, (2) pituitary, (3) sex, (4) adrenals, (5) pancreas, and (6) parathyroids.

(1) *The thyroid gland.*—The thyroid gland appears early not only in the embryonic life of the individual, but also in his family tree. It arises early in the vertebrate series

and becomes more and more highly developed the higher we go in the animal scale.

The effects of acute thyroid deficiency have been demonstrated by many observers who remove the gland from such laboratory animals as the rat, rabbit, and dog. Without citing specific experiments, the results of the operation can be summarized as follows: In young animals, there is a marked retardation of growth and development. Owing to the fact that the bones fail to calcify properly, the animals frequently have bowing of the legs. There is defective development of the brain, which is manifested by extreme difficulty in learning even the simplest thing. The sex organs remain small and fail to acquire normal function. Sex desire seems to be absent. There is defective tonicity of the muscles and the animal tires very easily. The body temperature is below normal. The skin is thick, dry, and scaly and the hair is commonly coarse and lusterless. The metabolism, on which the animal's energy depends, is markedly decreased: having thus a deficiency of energy, the animal is very sluggish, dull, and lethargic.

A striking illustration of the influence of thyroid on development is seen in tadpoles from which the glands have been removed. In these cases, the tadpole grows slowly but may become quite a large tadpole, yet it will never be able to change into a frog. One test of the potency of a thyroid preparation is its ability to turn tadpoles into frogs in a specified length of time. If normal tadpoles are given thyroid extract, they will become frogs in about one-third the time normally required. A frog fully formed but the size of a fly may thus be produced. By the use of this gland substance, it is possible in some instances to improve upon nature. For example, in the highlands of Mexico there lives a species of salamander that ordinarily suffers such a degree of thyroid deficiency that it never changes from the tadpole to the adult state, but continues from generation to generation as a gill-bearing tadpole. By the administra-

tion of thyroid extract, metamorphosis can be easily induced and nature's work thus completed.

If an overabundance of thyroid extract is taken into the animal body, either as the result of injections or as the result of feeding the animal thyroid substance, the following symptoms appear: The animal becomes restless, constantly moving about. The nervous system also seems to be so sensitized that the least stimulus will cause a violent reaction. The appetite is often excessive, but, owing to the marked increase in metabolism and in restless activity, the weight of the animal is usually decreased. If excessive amounts of thyroxin are given, a marked diarrhoea follows. The heart rate is increased and the blood pressure is elevated. The breathing is shallow and rapid.

Very few experiments have been made to test the effect of moderate amounts of thyroxin injections on the learning ability of animals, but it would appear that, when given in the proper amount, thyroxin increases the animal's ability to learn such problems as the maze. This result is probably due in part to the increased energy produced by the thyroxin, which causes greater activity in the animals. If the thyroxin is used in excessive amounts, the animal's energy discharge may be so disorganized that his rate of learning is impaired.

(2) *The pituitary gland*.—Since 1920, more has been found out about the pituitary than in all the time previous to that date. This gland, which lies at the base of the brain and, in man, is about the size of a cherry, is divided into two lobes, the anterior and the posterior, which differ both in structure and in function.

The posterior lobe is known to give out a secretion that has a marked influence upon blood pressure. When this part of the gland is deficient, the blood pressure is extremely low. The posterior lobe also has a good deal to do with the tonicity of the smooth muscles. An extract from it is used by obstetricians to contract the uterus after the delivery of

the child. Abel has succeeded in making a posterior lobe extract so potent that it will cause marked contraction in the uterus when applied in the concentration of 1 in 15,000,-000,000. This is equivalent to one grain dissolved in one thousand tons of fluid. In some of the lower animals, striking changes can be produced in the color of the skin by injecting extracts from the posterior pituitary. The posterior lobe is also known to have a close relationship to water metabolism. In cases of deficiency of this lobe, the kidneys excrete excessive amounts of water. Some people suffering from such conditions have produced as much as ten gallons of urine per day. The condition can be promptly relieved by injecting an extract from the posterior pituitary.

That the anterior pituitary secretes a hormone very important in growth has been known for a number of years. Philip E. Smith,⁽¹⁸⁾ of Columbia University, removed the pituitary glands of a number of rats with the following results: If the operation was performed on immature animals, they ceased to grow and retained the infantile condition throughout life. According to Smith,

Save for a reduction in their activity, and the fact that their hair was longer and less sleek than normal, observation of their external characteristics and behavior would not acquaint one with the fact that he was observing an animal perhaps some months instead of some weeks old.

When the operation was performed on adult animals, they developed a rough coat and an emaciated appearance. The condition could be corrected when anterior lobe tissue was grafted. If the animal was not given glandular preparation in some form, a gradual deterioration set in and death occurred long before the normal time. It would thus appear that the anterior lobe has a very close relation to longevity. This fact is borne out by clinical observations, for people suffering from pituitary disorders usually die relatively early. Following the destruction of the anterior

lobe, both the thyroid and the adrenals become unmistakably smaller. Smith's conclusions have been corroborated by many other investigators. It is known that deficiency in this lobe results in failure of growth, lack of sex development, and deficiency of the thyroid, the adrenals, and the sex glands.

In 1921 Evans and Long,⁽⁶⁾ of the University of California, demonstrated that simple water extracts of the anterior lobe of the pituitary glands of oxen, when injected into rats, consistently resulted in more rapid growth than was manifested by their untreated litter mates. At Harvard, Putnam, Benedict, and Teel⁽¹⁷⁾ succeeded in producing experimental acromegaly in dogs by giving excessive amounts of pituitary injection. This acromegaly was manifested not only in the overdevelopment of the lower jaw and the paws, but, in addition, the internal organs showed a marked overgrowth.

One of the most important hormones secreted by the pituitary is the sex or estrus-producing hormone. Several years ago, Evans found that when anterior pituitary grafts were implanted in experimental animals, there was a marked speeding up of sexual development, but that if growth hormone was given at the same time, this accelerating effect was prevented. Also, Putnam and Teel noted a suppression of sex activity in their acromegalic dogs—in spite of the fact that the genital organs were considerably enlarged. Their findings are borne out clinically, for women suffering from acromegaly usually fail to menstruate and lose the capacity for sex desire. In 1929 Fee and Parkes⁽⁷⁾ demonstrated that if the anterior pituitary was removed, ovulation did not occur, thus showing that the pituitary hormone is essential for ovarian function. It has also been found that in cases where estrus periods have remained absent as the result of pituitary removal, the estrus cycles can be reestablished by transplanting tissue from the anterior lobe. It was further found that when immature

female rats are injected with substance from the anterior pituitary, there is a marked increase in the size of the ovaries. Thus it appears that the anterior lobe secretes a hormone absolutely necessary for the normal sexual development and the maintenance of sex function in the animal. When the animal becomes pregnant, an excessive amount of the pituitary sex hormone is thrown off in the urine. One of the most reliable tests of human pregnancy is to take a few drops of urine from the woman and inject it into a non-pregnant female laboratory animal, either the rat or the rabbit. If the woman from whom the urine was taken is pregnant, definite changes will occur in the ovaries of the injected animal. If she is not pregnant, no changes will occur.

Riddle, in a series of experiments with monkeys at the Carnegie Institute of Washington, has demonstrated that the anterior pituitary secretes a milk-producing hormone. He was successful in isolating a small amount of this hormone, which he injected into castrated male monkeys and which caused not only enlargement of the breasts of the males but actual appearance of milk in their breasts.

(3) *The sex glands.*—Few glands in the body play as important a part in the personality make-up of the individual as the sex glands. On these depend the development of all the secondary sex characteristics and of sex desire. The horns of the stag, the mane of the lion, the development of breasts in the woman, the change of voice in man—all pay tribute to the secretions of the sex glands.

Inasmuch as the glands in the male and female have somewhat different functions, we shall consider them separately.

Castration of young males. From time immemorial, farmers have castrated domestic animals in order to improve the stock, to make the castrates take on fat more readily, or to make the animals easier to control for the purposes of labor. Castration has also been done in order to

produce greater tenderness in the meat. This is illustrated by the case of the capon. It is generally observed that the castrated animal has much less bodily vigor and energy.

With the revolving drum, it is possible to measure the spontaneous activity of the rat. In this situation, a normal young rat will sometimes run as much as eight or ten miles a day; but if the testes are removed, activity is markedly reduced. The results of such an experiment are graphically

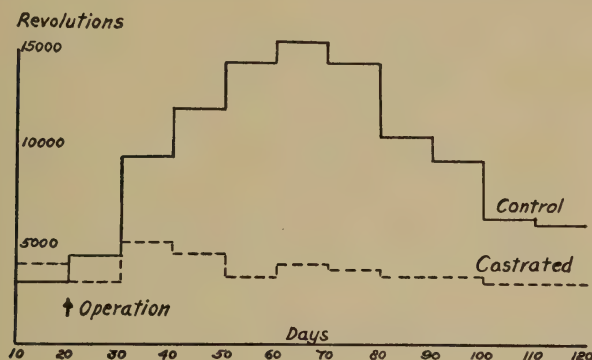


Fig. 19.—Graph Showing Effect of Castration on Activity of Rats. (After Hoskins.)

represented in Figure 19. It will be noted that at about the 60th day, when sexual vigor was at its height, the normal animals were about four times as active as their castrated brothers; but as age crept on, even the normal animals became much more sedentary. However, even at the end of the experiment, the normal animals were twice as active as the castrated group.

About twenty years ago, Steinach ⁽⁹⁾ removed the ovaries of female guinea pigs and replaced them with the testes of their masculine brothers, whereupon these artificial males outgrew their female controls, showed the skeletal characteristics, the coarser hair growth, and the pugnacity of normal males. Several experimenters have removed the

ovaries from chicks and transplanted testicles. In a short time, the artificial males developed combs and spurs and attempted to crow like the true males.

Castration of young females. The effects of deprivation of ovaries in the pre-pubertal stage are closely comparable to the destruction of the testes described above. The juvenile condition persists throughout life, and the animals remain sexually neutral. The accessory genital structures fail to develop properly, and the heat or estrus cycle completely fails to appear. If the castration is delayed until after puberty, the result is atrophy of the sexual organs and loss of procreative desire. In these animals, there is also a deficiency in the metabolic rate.

Complete destruction of the ovaries deprives the animal of the follicular and corpus luteum hormones. When the corpora lutea alone are removed, the most striking outcome is the interference with the processes of pregnancy. If the operation is performed early after the fertilization of the ovum, the embryo passes through the uterus without becoming implanted. If the operation is performed after the embryo has become implanted in the uterus, the pregnancy is interrupted and abortion follows. Occasionally a cyst is formed in the corpus luteum and persists for some time, in which case the animal never comes into heat and consequently is sterile so long as the cyst remains. When the cyst is removed, the estrus cycle recurs.

In 1923 Allen and Doisy ⁽¹⁾ succeeded in showing that the follicular fluid contains an effective stimulating substance. In their first experiments, they collected follicular fluid from the ovaries of hogs and injected it into the body cavity of rats weaned at the age of three weeks. This brought the young rats into a state of sexual maturity in three or four days, whereas it normally takes several weeks after the weaning age for the rats to become sexually mature. They also found that by injecting older animals from which the ovaries had been removed, they secured almost as

spectacular results. After injection, older castrated females whose genital apparatus showed marked atrophy and who manifested no interest whatever in their mates soon began to show considerable interest in the males, and in a short time the typical estrus cycle was reestablished. The castrated females accepted the males, but having no ovaries, they of course could not become pregnant.

It was thus demonstrated that the estrus cycle is initiated by the follicular hormone. This hormone has been crystallized in pure form by Doisy and named *theelin*. Doisy has been able to concentrate theelin of such potency that one gram would be sufficient to bring 2,000,000 castrated rats into heat. According to Hoskins,⁽¹²⁾ "If every woman and girl in the United States were as sensitive as a rat, one ounce of the preparation would suffice to evoke a reaction of the entire feminine population of this country."

(4) *The adrenals*.—The adrenal glands, two in number, are located one above each kidney. Important though these glands are in the higher animals, they are seldom found below the vertebrate level. In some species, such as the rat, there is a very marked sexual difference, the glands being proportionately larger in females than in males. Both structurally and functionally, these glands are divided into two parts: (1) the inner part, or *medulla*, and (2) the outer part, or *cortex*. The function of these parts will now be considered.

Function of the adrenal medulla. In all the higher animals, the adrenals play a major role in emergency situations. As a result of increased secretion from the adrenal medulla, the heart beats faster, the blood pressure is increased, and more blood sugar is liberated into the blood stream. The activities of the digestive tract promptly cease, and, due to a contraction of the walls of the blood vessels of the viscera, their blood supply is mostly transferred to peripheral structures. The blood vessels in the muscles relax instead of contracting. Even the composi-

tion of the blood is changed by the discharge of an augmented supply of sugar from the liver. The bronchioles of the lungs enlarge and the respiratory rate and depth are increased. There is increased tonicity of the skeletal muscles, and the whole animal organism is primed for strenuous action. As a result of these changes, the animal's endurance is increased and fatigue is decreased.

Some of Cannon's ⁽⁴⁾ experiments have made use of the power of adrenalin to affect smooth muscle outside the body. A cat was used as the subject, and a small amount of normal or "quiet" blood was withdrawn from a vein under local anæsthesia. This quiet blood was then allowed to flow about an excised strip of intestinal muscle connected with a writing lever so that all contractions were recorded. In quiet blood, the muscle contracted once, and then began to contract and relax rhythmically. The cat was then placed near a barking dog for five or ten minutes, during which time it became violently excited. Blood was again taken, and this "excited" blood caused almost immediate cessation of contraction in the isolated intestinal muscle. Cannon found further that by means of X-rays he could easily observe the rhythmical peristaltic movements in the stomach of a quiet and unexcited animal, and could see that when the animal became excited, the peristalsis stopped immediately.

This experiment is important in indicating somewhat the physiological action of adrenalin and its relation to emotions. In strong emotion, the sympathetic nervous system is active and in turn stimulates the adrenal gland to increased activity. The increase in amount of adrenalin in the "excited" blood was indicated by the cessation of contraction in the intestinal muscle. Here then we have a pair of glands stimulated to activity in times of strong excitement and by sympathetic nerve impulses which themselves produce at such times profound changes in the viscera. We have a secretion poured into the blood stream by

these glands which brings about the very changes in the viscera which accompany the major emotions and pain.

Functions of the adrenal cortex. Brown-Séquard, in a series of classic experiments in which he removed the adrenals from cats, dogs, guinea pigs, and rabbits, obtained the same results in all cases. Marked prostration was soon followed by death in each case. A short time later, two other investigators repeated Brown-Séquard's experiments on white rats, and found that all of their subjects survived the operation and were apparently little harmed by it. They attributed the fatal outcome of Brown-Séquard's experiments to bad surgery on his part. Several years later, the true explanation was discovered: namely, that the white rat has sufficient accessory adrenal tissue to be able to dispense with the glands proper. It is practically the only laboratory animal so equipped. Without the adrenal medulla, an animal may live indefinitely, but the loss of the cortex is invariably fatal. Animals from which the cortex is removed show a fall in metabolism, gastrointestinal upset, a fall in blood pressure, and a deficiency in blood sugar. They tire very easily, their appetite is markedly impaired or entirely lost, and their body weight decreases. In the mental sphere, there is confusion, apathy, and lack of interest in surroundings. As the condition progresses, the animal passes into a state of collapse and death is the outcome.

In 1929 Hartman made the first efficient cortical extract. About the same time, Swingle and Pfiffner,⁽²¹⁾ working independently, succeeded in making an extract by which they could keep alive indefinitely adrenalectomized cats. They could give an injection to a cat that had gone into a stage of collapse in which it could not move foot, head, or tail, and in a short time the cat would be up playing around, apparently none the worse for its experience. The changes that occur in these animals appear almost miraculous. The dead, or almost the dead, are brought back to life.

Animals deprived of the adrenal cortex find it quite difficult to endure changes in temperature. If subjected to cold, the body temperature goes down immediately. For example, Hartman ⁽¹⁰⁾ and his colleagues removed the suprarenals from a large number of white rats. They divided these subjects into two groups. Into one group they injected cortin, and into the other they injected an isotonic salt solution. These, together with a third group of intact normal animals, were carefully observed for differences in body temperature at 27° C. Little difference was found between the rats at this temperature. All the animals were then exposed to cold for three hours. At the end of this time, the experimental group that had been treated with cortical extract had decreased 2 degrees in body temperature, whereas the similar group treated with saline solution only had lost approximately 10 degrees. The temperature of the normal animals changed little, if any, under this treatment. The normal rats became active and remained so during the exposure to cold; the cortin-treated group were active during the early part of the cold period, but the untreated animals became quiet and lethargic. A similar experiment in which adrenalin was administered to one group of rats demonstrated the failure of this substance to enable the animals to maintain body temperature when exposed to cold.

The lack of adjustment to surrounding temperatures after removal of the suprarenals may be due to a decreased heat production or to an exaggerated loss of heat. Hartman and his colleagues determined the heat production in two groups of rats before and after the removal of the adrenals, and showed that one result of the operation was a distinctly lowered metabolic rate. However, when cortin was given following the removal of the glands, there was little change in heat production, but when the salt solution replaced the cortical extract, the energy metabolism fell. The effect of exposure to cold on the heat production was

then studied. In normal animals, the metabolic rate early in the cold period was increased 54 per cent, whereas in the animals whose adrenals had been removed and to which cortin had not been administered, the increase was only 17 per cent. It thus appears that a large part of the difficulty in the absence of the cortical hormone of maintaining body temperature during exposure to cold is due to failure to produce the added heat—a response that is apparently a normal one in the intact animal.

Paradoxical as it may seem, animals with marked deficiency in the adrenal cortex cannot endure heat. If there is a marked elevation of temperature, they easily become prostrated. The metabolic rate of these animals is also low. Immediately following the removal of the adrenals, the metabolism drops from ten to twenty per cent. Other interesting results of adrenal deficiency are its interference with growth and with the healing of wounds. Animals with marked adrenal deficiency grow extremely slowly or not at all. It is also interesting to note that these animals repair wounds very slowly. The wound-repair processes depend on cell growth. Both the healing of wounds and the stimulation of bodily growth can be induced by the administration of cortin.

Hartman has found that rats suffering adrenal deficiency have very low resistance to disease germs. Particularly was this true in the case of the typhoid toxin. He found that their resistance could be built up very materially by giving them cortin. It is interesting to note that following such diseases as influenza there seems to be a long period of convalescence in which the individual is “run down” and generally debilitated. He tires very easily, is subject to mental fag, and is devoid of his usual alertness and initiative. It would appear from the experiments of Hartman that such cases could be advantageously treated by the administration of cortin. There are probably two reasons why this glandular substance is not more widely used: first, relatively few

people know about it, since it was discovered only about three years ago, and second, and the more important reason, it is expensive to prepare. It is said to require about ten thousand dollars a year to buy a sufficient amount of the drug to keep alive a patient who has Addison's disease (tuberculosis of the adrenal gland). When the biochemists discover a less expensive method of procuring the substance, it will probably be one of the most widely used of all gland products.

(5) *The pancreas*.—Diabetes existed as a scourge to mankind long before man had any idea of its cause. Aretaeus, who wrote at about the first decade of the Christian era, gave an excellent description of the disease, but considered it "a melting of the flesh, which flowed away in the urine." It was not until 1890 that the true cause of diabetes was discovered, and its discovery well illustrates the importance of "a chance occurrence favoring an enquiring mind." The story, in brief, runs something like this: Naunyn, a German physician, while walking across a bridge connecting two wings of a hospital, happened to look at two packs of dogs playing in the yard below, separated from each other by a fence. The professor of physiology had removed the pancreas from one group of the dogs in a series of experiments that he was doing on digestion. He had separated these dogs from the other group. In noticing these dogs, Naunyn observed that swarms of flies gathered on the urine of the dogs whose pancreases had been removed, and not on the urine of the dogs of the control group. His curiosity being aroused, he acted on the hunch and, collecting some of the urine from the group operated upon, he proceeded to test it for sugar. Sugar was found in large quantities. It was clear that the dogs had diabetes. The unoperated dogs showed no sugar in the urine, and thus it was discovered that lack of pancreas causes diabetes.

Following this discovery, many investigators attempted to make a satisfactory extract from the pancreas, but more

than thirty years elapsed before success crowned their efforts. By January, 1922, a group of Canadian scientists, Banting, MacLeod, Best, and Collip, working at the University of Toronto, succeeded in making the extract that has meant the difference between life and death for thousands of diabetic victims.

In their experimental work, the dog was practically invariably used as the subject. That the pancreatic hormone is carried in the blood stream was demonstrated by experiments which showed that the blood of normal dogs contains substances that, when allowed to circulate through the system of a depancreatized dog, prevent the excessive accumulation of sugar in the blood and urine. Moreover, a pregnant bitch, deprived of her pancreas, does not develop diabetes as long as her fetuses remain in the uterus, indicating that the hormone produced by the fetal pancreases pass to the mother's blood stream through the placenta. Animals deprived of a pancreas are kept normal by daily injections of insulin (the pancreatic hormone).

When insulin is injected into a normal rabbit, the blood sugar, which normally stands at 0.115 per cent, falls rapidly and in an hour or two reaches the low level of 0.045 per cent. At this level, peculiar symptoms manifest themselves, namely, violent convulsive seizures that last several minutes and recur at frequent intervals, to be finally followed by the gradual development of coma and low temperature. These symptoms can immediately be relieved by an injection of a few cubic centimeters of glucose, subcutaneously or intravenously. In the case of a depancreatized animal, if large amounts of glucose are injected, the animal likewise goes into coma. It would thus appear that consciousness depends, in part at least, on the sugar content of the blood, and that when too great a decrease or increase of sugar occurs, unconsciousness follows.

The injection of insulin into normal animals apparently

increases the hunger drive. In the preceding chapter, Doctor Stone has summarized the work on the measurement of animal drives. At the present time, the author is directing a series of experiments designed to show how the strength of these drives can be influenced by the administration of certain chemical substances: for example, how much the hunger drive can be increased by the injection of the proper amounts of insulin (insulin causes a decrease in blood sugar); how it can be increased by injecting adrenalin (adrenalin causes increased blood sugar); how the thirst drive can be increased by the injection of normal salt solution; how the maternal drive can be increased by the injection of prolactin (a milk-producing hormone from the anterior pituitary); and how the sex drive can be increased by theelin (the estrus-producing hormone from the ovaries). This investigation is not sufficiently far advanced to report results at the present time, but the data now available clearly demonstrate that the strength of most animal drives is profoundly affected by the chemical condition in the animal's blood stream.

(6) *The parathyroids.*—The parathyroid glands in the human are four in number and lie just back of the thyroid. Some of the lower animals have six or more parathyroids, scattered in a variety of positions throughout the neck and upper chest. These glands are found in all vertebrates except the fish.

Parathyroid deficiency. Clear-cut evidence of the function of the parathyroids is seen in the acute deficiency following their removal. Within a few hours, the animal begins to show tenseness and fine tremors appear in the muscles; this condition tends to increase until, in a short time, convulsive movements that may at first involve but a single limb gradually spread to involve the whole body. The animal has reached the stage known as *tetany*. Tetany is due both to the increased muscular excitability and to the heightened irritability of the nervous system.

In some cases, instead of tetany developing, there is a most profound and progressive lethargy, accompanied by malnutrition and resulting in early death. No one knows just what determines which reaction will occur. The older the animal is, the less susceptible it is to parathyroid deficiency. An old animal may be deprived of three-fourths of his parathyroid tissue without showing marked symptoms, whereas a young animal will die if such an amount of parathyroid is removed. The symptoms that follow the removal of the parathyroids resemble those of a toxic condition—of such conditions as are seen in strychnine poisoning, rabies, or lockjaw.

Apparently, the most important factor in the production of tetany is disturbance in the calcium metabolism. When the glands are removed, a marked fall in the blood calcium follows, and when the animal goes into convulsions, the convulsive state can be checked by the injection of calcium salts, and, if the calcium is administered in sufficient quantities, all the symptoms of tetany can be held in check. It is known that calcium has a sedative effect on the nervous system, and it would thus appear that, by means of the ability of the parathyroids to mobilize calcium, we carry around with us in our blood stream a ready-made sedative.

Overactivity of the parathyroids. The effects of too much of the parathyroid hormone may be seen in normal animals that have been given injections of the hormone. A single dose causes the blood calcium to rise gradually for several hours. If the dose is excessive, the blood calcium may be doubled. Vomiting occurs and the blood shows an increased tendency to clot. If a massive dose is given, death will occur in two or three days. Repeated injections at short intervals of relatively small doses of parathyrin in normal experimental animals will cause death. In these conditions, the blood becomes so thick that it can scarcely pass through the capillaries, and cardiac failure follows.

Some animals are much more susceptible to this condition than others. Dogs and other meat-eating animals are particularly susceptible, whereas rabbits are not.

There are a number of questions concerning the effects of parathyroids on animal behavior that need investigation. One is the relation of the parathyroids to cell irritability. With some animals, distinct periods of lethargy are seen: for example, the hibernation of such animals as the hedgehog. It would be interesting to know whether there is excessive secretion of the parathyroid in these lethargic conditions. At other times, animals show an excessive responsiveness, and increased irritability. What, if any, of this increased activity is due to the lessening of the secretion of the parathyroids? Inasmuch as the parathyroids control calcium, it is natural to conclude that they have a lot to do with bone growth. Do such animals as the guinea pig, which develops very rapidly, have a much more efficient set of parathyroids than the human young, which develops so very slowly? Inasmuch as learning depends on irritability of the nervous system, and since the parathyroids are known to affect this irritability, what, if any, is the relation between the parathyroid secretion and the ability of animals to learn?

General consideration of the effect of chemical substances on behavior.—In Cannon's excellent book, *The Wisdom of the Body*, considerable attention is given to the various chemical balances that enable an animal to keep its behavior within normal limits. As Crile has so well pointed out, the animal is an adaptive mechanism. What are the things that aid most in this adaptation? One would readily select the nervous system as one of the main factors, but, beyond the nervous system, we find as most important the secretions from the ductless glands. How responsive are these glands to external forces? Is it the result of environmental forces acting on these ductless glands that produces mating in the spring and hibernation

in the winter? Not only are there external influences that affect these glands, but apparently certain internal rhythms and waves are initiated by them. Such periodic functions as sleep, menstruation, and the length of the gestation period are apparently controlled by glandular secretions.

Since the endocrines must depend on certain crude chemical substances for materials out of which to synthesize their products, it is pertinent to inquire into the part one's environment and food supplies play in the health and efficiency of his endocrines. It is known, for example, that cretinism and cystic goiter are much more prevalent in regions where the water is deficient in iodine. Since the chief parathyroid function is the mobilization of calcium, it is obvious that if too much or too little calcium appears in the diet, the activity of the parathyroids will be changed. Vitamin D has also a lot to do with calcium, but little attention has been paid to the relation of vitamin D to parathyroid function. Vitamin E is essential to reproduction, but few studies have been made on the effects of vitamin E on such glandular secretions as the sex-stimulating hormones from the pituitary or theelin and progestin from the ovaries. The environment in which man lives probably has a most important influence on his physiology, and his adaptation to this environment is facilitated by the responsiveness of his endocrine system.

(1) *Internal secretions and biological evolution.*—It is interesting to speculate about the part that the endocrines have played in evolution. The anterior lobe of the pituitary, the thyroid, parathyroids, and the endocrine cells of the pancreas all arise in the embryo from the digestive tract. It is not unlikely that originally these glands produced digestive juices, each with its own peculiar chemical make-up and specific function. In due course of time, the body developed adaptive reactions to these secretions and the glands became more and more specialized in the formation of these secretions until, by and by, they had

entirely lost their connection with the digestive tract. The theory that bodily reactions are secondary to glandular development is supported by the fact that certain animals produce hormones that have a marked influence on the organs of other animals, even though the animals producing them, themselves do not have these particular organs. For example, an extract from the posterior pituitary of the fish will cause the uterus of a cat to contract, but the fish has no uterus. The influence of glandular secretions on evolution is also seen in the case of the axolotl, which remains generation after generation a gill-bearing tadpole, but which when given the proper amount of thyroxin, changes to the adult form.

According to Keith ⁽¹³⁾ and Stockard, ⁽²⁰⁾ the hormones play a very important part in the development of racial characteristics. If we contrast the stature, for example, of the tall northern European with that of the dwarf-like African pigmy, we may conclude that the excessive height of the nordic is due to an over-secretion of the growth hormone of the anterior pituitary, and that the dwarfism of the pigmy is due to a deficiency in this hormone. Deficiency in the thyroid secretion causes general arrest in skeletal growth and marked changes in the structure of the cranium. The base of the skull fails to develop properly, so that the nose seems to be flattened and retracted between the eyes. Keith points out that these characteristics are especially prominent in the Mongolian face, and that the Negro shows somewhat the same characteristics. Some support is lent to this hypothesis by the fact that the basal metabolic rate of the Mongolian is slightly lower than that of the Caucasian. Skin color may also have an endocrine basis. In Addison's disease, for example, in which there is a deficiency of the adrenal secretion, there is an immense amount of pigment deposited in the skin. Because of this fact, Keith believes that the skin coloration of the Negro can be ascribed to a deficiency in the adrenal cortex. On

the whole, this idea of an endocrine basis for evolution is very speculative. Probably the best evidence that we have that the endocrines may affect evolution is seen in the experiments of Riddle that show that it is possible by selective breeding to produce rats characterized by very small pituitary glands, and races of doves characterized by large or small thyroid glands. His experiments show that nature could have used such a plan, if she had wished, to accomplish an evolutionary change.

(2) *Endocrines and senility*.—The subject that in all endocrinology has attracted the widest interest is the relationship of the glandular secretions to the onset of senescence. With an occasional man, old age comes on as early as 35. The hair begins to turn gray and fall out, the muscles weaken, desire fails, and both physical and mental fatigue seem to permeate his whole being. In other cases, we find men at 80 who still seem to have all the zest and vigor of youth. Just what part do the hormones play in causing this difference?

In 1918 an extensive report on the bodily changes in old age was made by Goodpasture.⁽⁸⁾ His study was made on 50 dogs, and he concluded that "with the continued increase in structural intricacy, incident to aging, the body cells gradually lose their metabolic equilibrium, so that the ultimate conclusion of cell differentiation is death."

The thyroid, pituitary, sex, and adrenal glands are known to control metabolism. The scantiness of hair, the dryness of the skin, and the tendency to chilliness so commonly found in the old are the typical picture of the deficient thyroid, and it is interesting to note that a microscopic section of the thyroid of an old individual shows considerable atrophy and replacement of the gland cells with connective tissue, which would give an anatomical basis for thyroid deficiency. In the same connection, it should be noted that Smith found the life span of laboratory animals from which he had removed the pituitary signifi-

cantly shorter than that of the control group. Lee has noted that rats that had had their pituitaries removed lost all their youthful activity. By the grafting of pituitary glands, these were brought back to normal. Steinach has shown that by certain surgical operations on the sex glands, the waning sex functions of an animal may be prolonged or rejuvenated. The relation of the ovaries to senescence is well known. In the case of the human being, when the ovaries are removed, there is a premature menopause, accompanied by genital atrophy, atrophy of the uterus and even of the breasts. When the operation is done on a young woman, her outlook on life soon becomes that of the typical old woman.

Sufficient has been found out about the endocrines in the last twenty years to indicate the very important part they play in animal behavior, but only a beginning has been made. There is no field in comparative psychology that offers more promise of worth-while findings than the relation of the glandular secretions to mental and physical efficiency. Trained investigators in this field are at present few, but more will surely be developed.

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CHAPTER VI

The Functions of the Receptors

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Vision

THE highest form of vision, permitting the perception of direction and of detail, is enjoyed only by animals having an eye that is equipped with some sort of optical image-forming apparatus. There are two types of such sense-organs, the "camera eye" possessed by vertebrates and certain mollusks, and the "compound eye" found in insects and crustaceans.

The efficiency of the camera eye depends upon the sharpness of the retinal image. In order that the image shall be distinct, the lens must have the proper form and the proper refractive characteristics. The receptor cells must lie in the plane where this image is cast. Since the distance of the image from the lens varies with the distance of the object, there must be a means for *accommodating* the eye, if the image is always to be sharp. Where the power of accommodation exists, it is usually achieved by an alteration in the shape of the lens, although in some cases, for example that of fishes and amphibians, the lens as a whole is moved towards or away from the retina. But these physical factors are not the only ones necessary for acuity of spatial discrimination and form perception. This acuity will obviously be limited by the fineness of the retinal mosaic, or in other words, by the number of receptor cells per unit area. If, as is generally the case, a whole

group of receptor cells is connected to the same optic nerve fiber, the number of *optic nerve cells* belonging to a unit retinal area will be the more significant factor. Other things being equal, the higher the magnifying power of the lens, the better the acuity of vision, since a given detail of the optical image will be spread over a larger number of retinal elements. In addition to these physical and retinal factors, factors in the central nervous system can play an important role in determining how sharply the animal sees and how well he makes use of his visual capacities.

In the human retina, there is a small central depression, the *fovea centralis*, in which the visual cells are smaller in cross section and are more densely packed together than in the rest of the retina. Moreover, each visual cell in the human fovea is connected with a separate fiber of the optic nerve, while in the outlying regions, a number of receptors share the same nerve fiber. Thus the fovea is a specially differentiated region of distinct vision.

A fovea is also found in the retinæ of apes and monkeys, of birds (some of which have two foveæ in each retina), and of certain reptiles and fishes. Where the characteristic foveal pit is absent, there may still be some rudiments of central differentiation in the form of a so-called *area centralis*. In animals possessing a central region of high acuity, eye movements of *fixation* may be observed: the eyes move in such a way as to bring the image of the object of interest upon this central area. In animals having binocular vision, the central areas play an important part in coördinating the two eyes. In the case of birds possessing a double fovea, one fovea is said to function in monocular vision, and the other (in collaboration with the corresponding fovea of the opposite eye) in binocular vision.

In the compound eye, a different principle of image formation is employed. The individual receptor cells, in an efficient compound eye, are small and closely crowded together, each being provided with a miniature lens of its

own. Only that light which passes in the approximate direction of the axis of the lens can affect the receptor cell; all other light is absorbed by a wall of black pigment which surrounds the cell. Each cell points in a slightly different direction from its neighbors, and thus receives light from a different small region of the external scene. Hence, there is an approximately point-for-point representation, or "image," of this scene on the receptor mosaic.

The usual stimulus for vision is sunlight reflected from the surfaces of objects. Sunlight consists of electromagnetic waves varying in length between about 250 and about 2,000 millimicrons (1 millimicron or $m\mu = 0.000001$ mm.). Of these the human retina is sensitive to only a small portion; the limits of visibility, defining what we call "light" in the narrower sense, are roughly 390 $m\mu$, at the violet end of the spectrum, and 760 $m\mu$, at the red end.

According to the most probable theory, the initial effect of light on the retina is the arousal of certain photochemical processes in the receptor cells. But the only energy that can be photochemically effective is that energy which is absorbed by the light-sensitive substances contained in these cells. The visibility limits we have mentioned are determined by the light-absorptive characteristics of this photochemical material. They represent the wave lengths below which and above which radiation passes through the receptor cell without suffering any absorption.⁽⁷⁾

In other organisms, the photochemical substances may be very different, and the visibility limits will then differ correspondingly.¹ It is known, for example, that the visual receptors of a number of animals respond to ultra-violet radiation which is far too short in wave length to be perceptible to the human eye. The eye of the fruit fly, as

¹In many cases, selectively absorbing media interposed between the responsive substances and the light may have an important influence on the spectral sensitivity. (Cf. Figure 21.)

Bertholf has recently shown, is sensitive to waves as short as $200\text{ m}\mu$, which do not exist in sunlight.

More significant information is obtained if one determines not merely the limits of spectral sensitivity, but the complete "visibility curve."^(7,4) The various wave lengths that lie within the sensitivity limits do not all have equal stimulating value. The light-adapted human retina is relatively insensitive to red or violet light; it is much more sensitive to wave lengths that are near the middle of its spectral range.

The relative "visibilities" of different wave lengths for the human eye may be measured if we determine for each wave length the least quantity of radiant energy that will give rise to a sensation of light. The *visibility* of a particular wave length is then, by definition, inversely proportional to its energy threshold. This would be a "threshold" method of measuring visibility. The so-called "visibility curve" is a graphical representation of the way in which visibility depends upon wave length.

Instead of a threshold method, a "matching" method has most often been used for the determination of the human visibility curve. In this case, the observer matches each wave length in turn, in regard to "psychological intensity," or brilliance, with some constant stimulus that serves as a standard. Visibility is then inversely proportional to the energy of spectral light that is required for the match.

The human visibility curve varies, in a very pronounced fashion, with the state of adaptation of the retina.⁽⁷⁾ It varies between two extreme forms, the one corresponding to a state of thorough adaptation to bright light, and the other to a state of thorough adaptation to darkness (Figure 20). The maximum of the first curve is at about $554\text{ m}\mu$, in the greenish yellow region, and the maximum of the second is at about $511\text{ m}\mu$, in the yellowish green region. This displacement of the visibility curve with changing

adaptation is called the "Purkinje effect." Its significance will be discussed below.

The threshold method has been applied by Watson ^(14,4) and by Honigmann ⁽¹⁰⁾ to the determination of the visibility curve for chickens. In Honigmann's procedure, a narrow band of spectral light of a chosen wave length illuminated

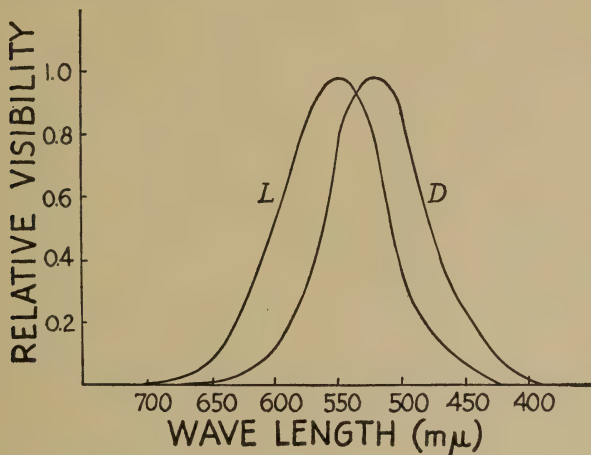


Fig. 20.—Human visibility curves. *L* is the visibility curve of the light-adapted human eye. (Standard visibility data of the Optical Society of America.) *D* is the visibility curve of the dark-adapted human eye. (After Hecht and Williams.) In each curve the maximum visibility is arbitrarily given the value 1.

a single row of rice grains among a number of similar rows that lay in darkness. The energy of this light, beginning at zero, was gradually increased until the birds began to peck at the illuminated grains. (The unilluminated grains were left untouched by the birds.) The visibility curve calculated from the thresholds is broadly, though not exactly, similar to that of man; and, as in man, the visibility curve varies with the state of adaptation, that is, the chicken displays the Purkinje effect.

Laurens⁽¹²⁾ has studied the sensitivity of alligators and pigeons to the different spectral wave lengths, employing the amount of *contraction of the pupil* as an indicator. Figure 21 represents the results that he obtained with light-

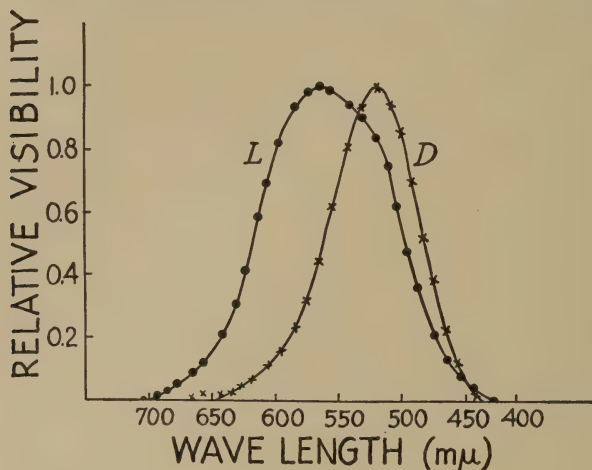


Fig. 21.—Curves showing the relative amount of pupil-contraction produced by different spectral wave lengths acting on the eye of the pigeon. (After Laurens.) Curve *L* is for light-adapted and curve *D* for dark-adapted birds. Note that the pigeon is relatively insensitive to light of short wave length. The retinae of birds and reptiles contain colored oil globules that absorb the blue and violet rays and thus prevent them from stimulating the receptors.

and dark-adapted pigeons; the presence of a Purkinje effect and a general resemblance to the human visibility curves will be noted.² Laurens also found a Purkinje effect in alligators.

² Laurens's procedure was to keep the energy of the light constant and measure the size of the pupil under illumination by different wave lengths. His curves are not true "visibility curves" in the sense of our definition, but they are probably not greatly different from the true curves.

True visibility curves would be obtained by measuring, for each wave length, the quantity of energy required to produce the *same* degree of pupillary contraction, and then plotting the results in the manner we have described above.

Very little adequate work has been done on the spectral sensitivity of animals, and apparently none at all on that of the infra-human mammals. A rough idea of the extent and character of visibility for a given animal may be obtained by observing responses to colored papers, colored glasses, and so forth; but the results have little significance except in so far as one can compare them with the responses of the human subject, or of some other organism, to the same stimuli. They do not furnish an adequate substitute for energy measurements with spectral lights.

Schlieper ⁽¹³⁾ has worked out an ingenious technique using colored papers which he has applied to a variety of animals. This method makes use of the compensatory reactions (movements of the eyes, head, or entire body) which the animal displays when it is placed inside a rotating drum whose walls are covered with alternately light and dark striations. If one set of stripes is colored and the alternating set consists of a gray which, for the animal's eye, is equally brilliant, the reaction is absent. (This is true even though the animal may have color vision.) By using different shades of gray in turn, one can find a gray that will match the given colored paper according to this criterion. The matches can then be compared with those obtained with other organisms, including the human being.

The human retina contains two types of photoreceptors: the rods, which are most numerous in the periphery and become progressively less numerous towards the center, and the cones, which are most densely distributed in the center and decrease in number towards the periphery. There is a small central region that contains only cones (the "rod-free area").

According to the "duplicity" theory of von Kries, the cones and rods differ in their mode of function. Sensations of color are mediated only by the cones, the rods being "totally color-blind." The enormous increase in retinal sensitivity that comes with adaptation to darkness or to

dim light is primarily a function of the rods. When the illumination is very weak, therefore, only the rods are excited, and no colors can be discriminated. The cones and rods also differ in their relative responsiveness to different wave lengths of light. The cones are maximally sensitive at $554\text{ m}\mu$, while the rods have their greatest sensitivity at $511\text{ m}\mu$. The two curves of Figure 20 describe the visibility relations for *cone* and *rod* vision respectively. The Purkinje effect represents the shift in the visibility curve of the eye that accompanies the transition from cone vision to rod vision in the course of adaptation.

The duplicity theory is supported by an impressive array of facts from human vision. Of particular importance is the fact that the Purkinje phenomenon does not appear in the rod-free area of the retina. It is also completely lacking in totally color-blind persons, as well as in certain individuals who are congenitally "night-blind" or lacking in the normal power of adaptation to darkness; in the first group, there is apparently a complete absence of cone function, and in the second, an absence of rod function.

Another line of evidence for the theory is furnished by the comparative anatomy of vertebrates. In general, mammals of nocturnal habits (bats, moles, mice and guinea pigs) have only rods in the retina, or, at any rate, very few cones. Dogs, cats, and rabbits have relatively more rods than does man. The retinæ of "night birds" are richer in rods than those of "day birds." Among the reptiles, those of diurnal habits (snakes, lizards, and chameleons) have few, if any, rods, while the nocturnal gecko possesses no cones. A similar correlation appears in the fishes; in particular, the retinæ of deep-sea fishes contain only rods.

The duplicity theory has received further striking confirmation from the work of von Frisch ⁽⁶⁾ on light- and dark-adapted fishes. In normal daylight, the fishes that he studied possessed color vision, and could be trained to respond selectively to a particular color stimulus as op-

posed to a gray of any shade. If, however, the illumination was gradually reduced, there came a point where the fishes, while still able to see, no longer made any discrimination between colored and gray objects. In other words, they became totally color-blind, as the normal human being does under analogous conditions.

In parallel with the transition from color vision to total color blindness, von Frisch discovered that certain characteristic changes took place in the microscopic structure of the fish's retina. It has long been known that the visual receptors of the fish, and of certain other organisms, change their position in the retina according to the intensity of the light. In the retina of a fish that has been adapted to bright light, microscopic examination discloses, according to Von Frisch, that the cones lie in the plane of the optical image, while the rods have retreated back of this plane and are buried in the black retinal pigment. In a dark-adapted fish, on the other hand, the rods lie in the plane of the image, and the cones have been pulled away from the light. At intermediate states of adaptation, both cones and rods are found in the image plane; as the illumination is progressively weakened, more and more cones retreat until finally, at a certain critical illumination, only the rods remain. Moreover, the behavior experiments indicate that the fish loses its power of *color* discrimination at this same critical illumination.

In no case has color vision been found in a vertebrate whose retina is completely devoid of cones; nor has a Purkinje effect been demonstrated except in animals equipped with both types of retinal element.

Color Vision

Before we enter into the question of color vision in animals, let us first consider what we mean by "color." It is important to realize that "color" is, in the strict sense,

a psychological rather than a physical concept. The word refers to the phenomena that the human subject experiences when his eyes are stimulated by light, and not to any property or characteristic of the light waves themselves.

All we have on the physical side is a wave motion having a certain wave length (or frequency) and a certain energy value. Or, as is usually the case, we have a mixture of waves, each having its own wave length and energy value. When light waves strike the human retina and the effect is transmitted to the brain, color sensations are aroused according to certain definite laws.

The laws relating stimulus and sensation, however, are by no means simple. This fact becomes evident when we consider the phenomena produced by the *mixture* of different kinds of light. For example, we can mix spectral yellow light with spectral blue light in a certain proportion and produce *white*. In other words, the sensation we obtain from this mixture of two wave lengths is similar to that which we obtain from ordinary sunlight. We can also mix spectral red light with its complementary wave length in the blue-green region of the spectrum and again produce a mixture that matches sunlight. Or, we can take three wave lengths, from the red, green, and blue regions of the spectrum, and once more obtain a white-appearing mixture. Here we have four mixtures of light waves which, considered from the purely physical standpoint, are extremely unlike: namely, (1) a pair of complementary wave lengths, (2) a different pair of complementary wave lengths, (3) a mixture of three wave lengths, and finally (4) sunlight, which is a mixture of *all* the visible waves in certain characteristic proportions. So far as the eye is concerned, these four different stimuli are exactly equivalent; they all look "white." This shows us very clearly that there is not a simple one-to-one correlation between stimulus and sensation, but that the same sensation can be produced in a

great number of different ways. The explanation of this fact can be given only by a theory of the physiology of human vision. The important point for us to bear in mind is this: that when we speak of "white" light, "red" light, "blue" light, and so on, we are describing light in terms of its effects on the human subject rather than in terms of its own properties. Custom and convenience sanction such terminology, and there is no harm in it provided we are clear about its real meaning.

When we say, for example, that "the eye of an animal was stimulated with yellow light," we mean that the animal was stimulated with a wave length, or mixture of wave lengths, that arouses the sensation of yellow in the human observer. We have not really described the actual stimulus until we have stated exactly what wave lengths it contained and their relative energy values. In experiments on human vision, it may often be sufficient to describe a stimulus in terms of its *appearance* for the normal human subject; but when we are dealing with an animal, which may possess a visual system quite different from our own, there are many chances of falling into error if we do not distinguish clearly between "*color*" and *wave-length composition*. Much experimental work has been vitiated because of the confusion of thought which the very use of the term "color" so frequently induces.

Speaking precisely, we have no means of determining whether animals "have color vision" or "discriminate colors," because colors are sensations, and to the animals' sensations we have no access. If we ask whether they can make a certain definite sort of *discrimination* between different light stimuli, we are asking an answerable question. We can still use the term "color vision" in conformity with usage—but we shall mean by it the ability to make this particular type of discrimination.

What is to be our criterion of color vision? Let us consider, for a moment, the case of a human being having the

rare abnormality of "total color blindness." Light stimuli acting on his eye give rise to sensations that may differ in brilliance, but in no other respect. Any two stimuli, regardless of their wave-length composition, may be made to produce exactly identical sensations for him provided their physical intensities (energy values) are so adjusted that there is no *brilliance* difference for his eye. In the normal subject, we have a different state of affairs. A red and a yellow may be made to match in brilliance, but the characteristic *hue* difference between redness and yellowness still remains.

Turning to the case of the animals, we can state the following criterion: An animal has color vision if it can be caused to display a discrimination between stimuli of different wave-length composition, and if this discrimination *cannot be made to disappear* by changing the proportion between the physical intensities (energy values) of the stimuli.³

Suppose that we train an animal to "choose," for example, spectral blue light, of wave length 470 $m\mu$, in preference to spectral yellow light, of wave length 580 $m\mu$. Suppose we also find that the animal chooses the first light as opposed to the second no matter how much we

³ In experimental work on the problem of color vision, certain fallacies have sometimes been committed. For example, the assumption has been made that an animal has "color vision" if it can discriminate between stimuli of different wave-length composition that look equally bright to the human eye. But if the visibility curve of the animal differs from that of man, lights that have equal stimulating power for the human eye will, in general, have unequal stimulating power for the eye of the animal. To use anthropomorphic language: two differently colored lights appearing equally bright to man are not necessarily equally bright for the animal. The animal may therefore be able to discriminate them, regardless of the presence or absence of "color processes" in its retina.

We cannot define color vision as the capacity to discriminate between dissimilar lights that are equated in terms of *energy value*; this fact is at once obvious when we consider the significance of the visibility curve.

vary the relative intensities of the two lights. We conclude that the animal has color vision.

We do not yet know what sort of color vision the animal has, nor how much resemblance there is between his type of color vision and that of man. Our next step must be to determine just what discriminations the animal can make and what discriminations it can *not* make. For this purpose, it is better to employ single wave lengths of spectral light as our stimuli, rather than the complex or mixed radiations furnished by colored glasses or colored papers.

We may proceed to determine the *least difference* in wave length that the animal can discriminate. In the human subject, the ability to distinguish small wave-length differences varies, in a pronounced way, in the different parts of the spectrum. Under favorable conditions, a difference as small as $1\text{ m}\mu$ between two wave lengths in the yellow region may be distinguished, while a difference of $20\text{ m}\mu$ or more between two red spectral lights fails to be recognized. A study of the manner in which the wave-length threshold varies in the different regions of the spectrum gives a valuable indication of the type of color vision that we have to deal with. If an animal's wave-length threshold varies in the same fashion as that of man, the presumption is that its receptor system is also similar to our own.

Two single wave lengths that differ by less than a threshold amount may be called "equivalent stimuli" for the animal. But there is another case in which different stimuli may produce identical effects on the animal, and this is the case where we deal with *mixed* radiations rather than radiations of a single wave length. We have already seen that the same effect, namely, the sensation of whiteness, may be produced in human vision by a variety of different wave-length mixtures. The same thing is true for chromatic sensations. If there is any analogy between the vision of man and that of the animal, we should expect the animal to display the same peculiarity; in other words, we

should expect that the animal would manifest *no discrimination* between certain wave-length mixtures of very unlike composition.

A second important problem, therefore, is to determine what wave-length *mixtures* are equivalent stimuli for the animal. These phenomena of light mixture are of fundamental importance for the theory of human vision, and they are equally important for any interpretation of animal vision.

We must take warning not to assume the solution of this problem in advance. Too often it is assumed, without sufficient ground, that any lights that appear similar in color to the human eye will also be equivalent stimuli for the animal's eye. Comparatively little attention has been paid to the actual testing of this point. As a matter of fact, the assumption is probably correct—within limits—in many cases, although there must be other cases in which it is very definitely incorrect.

One example of the latter type is furnished by animals whose receptors are sensitive to *ultra-violet* light. If the ultra-violet rays are filtered out of ordinary sunlight, the human being notices no difference; the filtered and unfiltered lights are equivalent stimuli for man. On the other hand, the small crustacean *Daphnia*, which is sensitive to ultra-violet, behaves quite differently towards these two kinds of light:⁽²¹⁾ they are not equivalent stimuli for this organism.

Experimental work on the color vision of animals has revealed in certain forms a type of discrimination that is very much like that of man, while in other forms there is either no discrimination at all, or a type of discrimination that differs from our own in important ways. In a number of animals, the bare fact of color vision has been established but very little is known about the details of this color vision.

Trendelenburg and Schmidt ⁽³⁰⁾ have recently performed careful experiments on monkeys (*Macacus rhesus* and *Pithecius fascicularis*) with spectral light. Figure 22 represents the results of a typical experiment on wave-length discrimination employing the following technique: The animal was trained to take food out of a box when the box was illuminated by a beam of wave length $535\text{ m}\mu$, and to

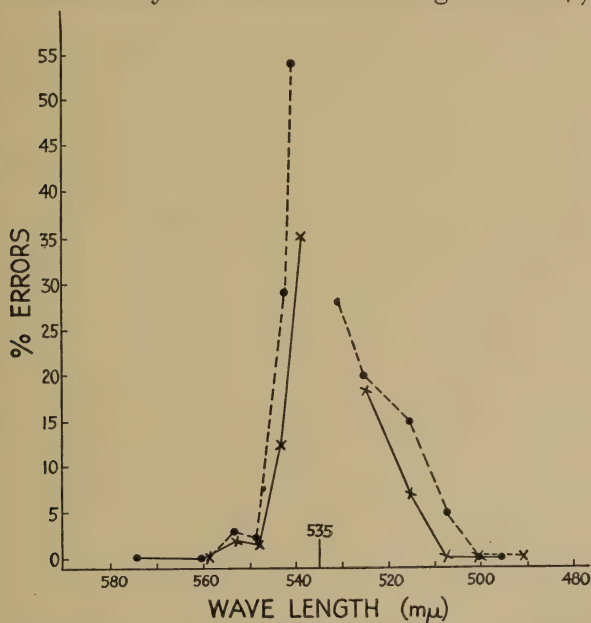


Fig. 22.—Showing the percentage of cases in which confusions were made between a standard light of $535\text{ m}\mu$ and lights of longer and shorter wave length. The solid line represents results from tests of a monkey, the broken line from tests of a human being. (After Trendelenburg and Schmidt.)

refrain from responding when the illumination had a different wave length. After thorough training, tests were made in order to determine how precisely the animal could distinguish the training light from lights of neighboring wave length. Figure 22 indicates the percentage of cases in

which various stimuli greater or less in wave length than $535\text{ m}\mu$ failed to be differentiated from this training light (graph drawn with solid line). The graph drawn with broken line shows the results of discrimination experiments carried out under analogous observing conditions on a practised human subject. It will be noticed that the two "error curves" are very similar in form; this fact points to a similarity between the two types of vision, which was confirmed by further experiments. It will also be observed that the monkey is more sensitive to slight wave-length differences than the human subject.

Although the monkey and the human being differ in the fineness of their wave-length discrimination, it was found that the *variation* in sensitivity from one spectral region to another is of the same type in both cases. In the yellow region, where man's wave-length discrimination is especially good, the monkey's is also good, and in the green region, both man and monkey display relatively coarse discrimination.

It was also found that the phenomena of light *mixture* are quite similar for the monkey and the human being. For example, two spectral wave lengths that are complementary for man are also complementary for the monkey; that is, their mixture is indistinguishable from ordinary "white" light. In human vision, a spectral yellow can be matched by a mixture of spectral red and green; and the same mixture is responded to by the monkey as if it were identical with the spectral yellow.

The experiments of Wolfgang Köhler ⁽²³⁾ and of Ladygin-Kohts ⁽³²⁾ point to the existence of color vision in apes (chimpanzees); presumably the color vision of these animals resembles that of monkeys and human beings.

Our knowledge about the color vision of other mammals is rather scanty. The indications are that certain of these lower mammals have color vision of a sort; but that, even where color vision is present, it is of little or no biological

importance to the animal under natural conditions. This means, incidentally, that experimentation on color vision in these forms is subject to peculiar difficulties.

In the case of dogs, the experiments of Samojloff and Pheophilaktowa,⁽²⁷⁾ and, later, of E. M. Smith⁽²⁹⁾ have indicated the presence of a certain weak color vision, permitting a rather gross type of discrimination under experimental conditions. Bierens de Haan and Frima,⁽¹⁶⁾ working with lemurs, and Hopkins,⁽²²⁾ working with mice, have obtained similar results.

Von Hess⁽²¹⁾ has applied to the dog his ingenious physiological method of testing for color vision by means of the responses of the pupil. This method employs the following principle: In a normal human being, the reactions of the pupil depend upon color as well as upon intensity of light. If the retina is alternately stimulated by two lights of equal brilliance but different color, the pupil contracts at each alternation. This phenomenon is absent in the totally color-blind subject. Applying the method to the dog, von Hess found that there is a specific effect of wave length upon the pupillary reactions, but that this effect is much weaker than in man. He infers that colors appear to the dog in a very low degree of saturation.

We should expect to find, at the best, only weak color vision in animals which, like the dog and the mouse, and the nocturnal lemurs studied by Bierens de Haan and Frima, have only a small number of retinal cones. In the case of the rat, the experiments of Munn⁽²⁵⁾ and of Coleman and Hamilton⁽¹⁷⁾ point to total color blindness.

Color vision in birds of diurnal habit (pigeons and chickens) has been demonstrated. Hamilton and Coleman⁽²⁰⁾ have found that the pigeon's discrimination of spectral wave lengths is broadly similar to that of the human being, and that the wave-length thresholds are of the same order of magnitude.

Color vision has been found in certain fishes. The color responses of the minnow and the stickleback have been most thoroughly investigated, by Schiemenz ⁽²⁸⁾ and by Wolff. ⁽³¹⁾ These fishes have been shown to possess a remarkably differentiated mechanism for color perception. In training experiments, one can readily establish a response to a particular wave length which is unaffected by variations of intensity. The fish is fairly sensitive to small differences in wave length. The wave-length threshold is lowest in the yellow, that is, in the same spectral region where human discrimination is also sharpest; and there are a number of other broad resemblances between human discrimination and that of the fish. For example, a fish that has been trained to respond to red spectral light will occasionally confuse a *violet* light with the training light; and vice versa. In our vision, these two kinds of light arouse sensations that are similar, though not identical, in hue; the fact that the fish makes these particular confusions suggests that his sensory mechanism has characteristics in common with ours. There are also some indications that phenomena of *light mixture* are to a certain extent similar for fish and man. ⁽¹⁸⁾

Nevertheless, there is an important difference between the two types of vision, inasmuch as the fish responds not only to the wave lengths that are visible to man, but to the ultra-violet wave lengths as well. A fish that has been trained with ultra-violet light discriminates this light from violet, blue, or any other spectral stimulus.

Turning to the invertebrates, we find that the honeybee possesses a very well-developed color sense. The color vision of this insect has been studied by Von Frisch, and by Kühn ⁽²⁴⁾ and Pohl. Like the first, the bee is easily trained to associate a particular spectral wave length with food, and shows no confusion if the intensity of this light is changed. (As a matter of fact, according to Kühn and Pohl, it is *im-*

possible to train the insect to respond selectively to a particular absolute intensity of light.)

The honeybee, like a great many other insects, is sensitive to ultra-violet light, although its eye does not respond at all to red light. Its wave-length discrimination has been studied; it may be concluded that the color processes in the bee's receptors are of the same order of complexity as those in the human receptors, although considerably different in type. Kühn and Pohl infer that the bee perceives four different "color-sensation qualities" in its total spectrum, one of these qualities corresponding to the ultra-violet.

Kühn was able to demonstrate the interesting fact that the phenomenon of *simultaneous contrast* occurs in the vision of the bee. Insects were trained to seek food at a place marked by a ring of blue paper. In the test experiments, a *gray* ring on a *yellow background* was substituted for the blue, and presented without food. The bees immediately flew to this ring; and careful control tests indicated clearly that this was a genuine case of simultaneous contrast—in complete analogy to the familiar fact of human vision that a gray area on a colored background acquires a tinge of the complementary color.⁴

Fruitflies⁽¹⁹⁾ and butterflies⁽²⁴⁾ have been shown to possess color vision, but of a simpler type than the bee's. The responses of these insects display a certain analogy to those of "partially color-blind" human beings. Such persons see only two hues in the spectrum, all the long waves appearing yellow to them, and all the short waves appearing blue. The color sense in butterflies and fruitflies seems to be equally simple. However, the analogy is far from complete; for example, these insects, like the bee, are sensitive to ultra-violet light.

For bees, fruitflies, and a number of other insects, ultra-violet has a peculiar attraction; a beam of this "invisible"

⁴ Révész, ⁽²⁶⁾ employing a similar method, has demonstrated simultaneous contrast in chickens.

light quickly draws a swarm. It seems probable that this attraction is due to the specific action of this kind of light on the color receptors—or, in anthropomorphic language, to the specific “color” of this light for the insect’s eye.

Among the crustaceans, the most complete investigation has been made on waterfleas (*Daphnia*) by Otto Koehler.⁽²⁴⁾ He employed an interesting method which required no training of the animals, but which made use of an unlearned tendency to seek certain wave lengths and avoid others (a “chromotropism”) that these animals display. Like the insects we have just mentioned, *Daphnia* has a simple type of color vision, broadly analogous to the “dichromatic vision” of partially color-blind human beings. *Daphnia* also responds to ultra-violet light. In spite of the many dissimilarities between human color vision and that of *Daphnia*, Koehler found two remarkable similarities: A pair of spectral lights that are complementary for the human eye are also complementary for the eye of *Daphnia*. Also, *Daphnia* displays a phenomenon analogous to “successive color contrast” or “negative after-images” in man. An exposure to colored light seems to leave an after-effect, so that if a white light is now presented, the animals respond to the latter as if it were “oppositely colored.”

The researches of the last ten years have shown that color vision is a much more widespread phenomenon in the animal kingdom than had usually been supposed. Experiment has rather surprisingly revealed a capacity for color discrimination in numerous animals for which, to all appearances, this capacity is of little or no biological advantage. Moreover, it is by no means a universal rule that the “higher” animals have the more elaborate color sense.

Despite many striking divergencies between the color responses displayed by different animals, we find certain equally striking resemblances. Particularly significant are the similarities we have noted in respect to the “equivalence” of stimuli; wave-length mixtures that act similarly

on the human receptors are also found, in various instances, to be equivalent stimuli for the receptors of animals. This fact seems to indicate that these different sensory mechanisms have a certain fundamental ground plan in common, although they may differ radically in details; and it is a fact of obvious importance for the general theory of color vision.

Hearing

Before we can profitably discuss the problem of hearing in infrahuman animals, we must have a clear notion of just what we mean by "hearing." In our own case, we have no difficulty: the air vibrations emitted by a tuning fork, a bell, or a buzzer, give us certain characteristic sensations, which we call sensations of sound. As a matter of fact, however, vibrating bodies often arouse in us a different type of sensation, in addition to that of sound. If we place our hand on the top of a piano while a note is being struck, we can "feel" the vibration of the wood. The same vibrating source arouses a response in two sets of receptors, the hair cells of the cochlea and the receptors of the skin. The two kinds of response are usually fairly easy to differentiate from one another, by both introspective and physiological criteria.

In the case of animals, we must depend on a physiological criterion. When we say that an animal has a sense of *hearing*, we must mean not merely that the animal displays response to vibratory stimuli, but that this response is mediated by receptors which are distinct from those of tactual sensitivity, and which are specially adapted for response to vibrations of the fluid medium (air or water) in which the animal is immersed.

Assuming that we have established, by properly controlled experiments, that an animal has an auditory sense according to our criterion, we are then faced by a number of problems analogous to those that confront us in the study of vision. In all cases, the auditory receptors respond only

to wave frequencies within a certain range; there are upper and lower "limits of hearing" analogous to the limits of vision with spectral light. In man, the limits of hearing are roughly 20 and 20,000 vibrations per second; but in animals, quite different limits may be found. Certain insects, for example, hear sounds that are too high in frequency to be perceptible to the human ear.—In the cat, according to Wever,⁽⁴⁵⁾ the upper limit is about the same as in man.

Moreover, different frequencies lying within the range of audibility will differ in their stimulating value for the animal's receptors, even though their physical intensity (energy value) is held constant. In other words, there is an "audibility curve" analogous to the "visibility curve." In man, these two curves are roughly of the same form. Just as the human eye is most sensitive to light waves of medium wave length (or frequency), and is less and less sensitive to wave lengths that depart more and more from this medium value, so also the ear is relatively insensitive to very low or very high frequencies, and its response becomes progressively stronger as a certain middle frequency is approached. The point of maximum sensitivity is at about 2,000 vibrations per second.

Horton⁽³⁸⁾ has found that the audibility curve of the guinea pig does not differ greatly from that of the average human subject. As yet, such tests do not seem to have been made on any other animals.

We have a further problem in hearing which is analogous to that of color discrimination in vision: namely, the problem of *frequency discrimination* ("pitch discrimination"). A human being with normal hearing can distinguish a sound of high frequency from one of low frequency even though the two sounds seem equally loud to his ear. A completely "tone deaf" person cannot make such a discrimination; he perceives only differences in loudness, and not differences in pitch. If we present such a person with two stimuli of different frequencies, he may report that one

seems louder than the other; but if we now progressively increase the energy of the weaker sound, he will eventually report that the two are indistinguishable. Generalizing, we say that a human being or an animal has pitch discrimination if it can differentiate between frequencies independently of the energy of the waves. We cannot infer pitch discrimination until we have eliminated the possibility of discrimination on the basis of mere intensity.

The fact that an animal may show discrimination between sounds of different frequency that have equal *loudness* for the human observer is not sufficient to prove pitch discrimination, for the audibility curve of the animal may differ considerably from that of man. Again we have a situation similar to that which confronts us in the study of color vision. In both cases, the standard procedure is to attempt to establish a discrimination between two stimuli of different frequency (or wave length) and then, if this is successful, to determine whether the same discrimination manifests itself when the intensities are radically changed.

Our knowledge regarding hearing in animals may be briefly summarized as follows. In mammals and birds, we have clear evidence, both experimental and anatomical, for the existence of an auditory sense. Hearing has also been demonstrated in certain reptiles (lizards), amphibians (frogs ⁽⁴⁹⁾ and toads), and fishes; among the invertebrates, a true auditory sense is found only in a few insects. At the present time, we have evidence for *pitch discrimination* in only a very few animals. Anrep ⁽³³⁾ finds that the dog can discriminate frequencies without regard to intensity; Upton ⁽⁴²⁾ reports that the same is true of the guinea pig. The skilful imitation of sounds which is displayed by parrots, jackdaws, canaries, and other birds indicates pitch discrimination of a high order. Jellinek ⁽³⁹⁾ reports that turtledoves can distinguish two notes that are only a semitone apart. Finally, a certain gross frequency discrimination has recently been demonstrated in fishes.

In the cochleæ of mammals and birds, we find a basilar membrane essentially similar to that of man (although in the birds this membrane is considerably shorter than it is in mammals). Animal experimentation has provided one of the most valuable means for testing theories of the action of the basilar membrane and, in general, of the auditory mechanism.

Many theorists, following Helmholtz, suppose that the basilar membrane functions as an "analyzer." When a particular frequency of wave motion is conveyed to the fluid of the internal ear, then, according to this conception, only a limited area of the basilar membrane is set into vibration. Each fiber of the basilar membrane is assumed to be "tuned" to a particular frequency of vibration, a response being evoked only from those fibers that are in tune, or approximately in tune, with the stimulating tone.⁵

Other theories have been proposed which do not assume the principle of resonance, or the notion that the response to a particular frequency is localized at one particular region of the basilar membrane. There is a variety of these non-resonance theories, but most of them have one important feature in common: they assume, in order to explain the possibility of *pitch discrimination*, that the *frequency* of the stimulating tone is somehow represented in the stream of nervous impulses that is transmitted from cochlea to brain. With the Helmholtz theory, such an assumption is unnecessary. A tone of higher or lower pitch will, according to this theory, set a different region of the basilar membrane into vibration, and will thus cause impulses to travel up a different set of auditory nerve fibers. The recognition of pitch depends upon *which* nerve fibers are carry-

⁵ There are certain modern analytic theories of hearing that introduce different mechanical principles from those assumed in the "harp theory" of Helmholtz; but they agree with Helmholtz's theory in maintaining that tonal stimuli give rise to a more or less localized response of the basilar membrane.

ing impulses, and not upon the nature of the nervous impulses themselves.

Held and Kleinknecht ⁽³⁷⁾ have performed experiments on the guinea pig that were designed to put the Helmholtz conception to a critical test. By means of an extremely fine drill (0.1 mm. in diameter), they bored a small hole through the bony wall of the cochlea so as to break a few threads of the spiral ligament that holds the basilar membrane in tension, but without allowing any of the fluid of the cochlea to escape. According to the Helmholtz theory, the basilar-membrane fibers behave like the stretched strings of a harp; if certain particular fibers are slackened, these fibers will no longer resonate to vibrations of the cochlear fluid. Relying on this theory, therefore, we should expect the operation to make the guinea pig deaf to a certain small range of frequencies while retaining normal response to all other frequencies. Moreover, we should expect an injury near the base of the cochlea to cause deafness to relatively high tones, and an injury near the apex to cause deafness to relatively low tones, for the basilar fibers are shortest at the base of the cochlea and longest at the apex.

These expectations were confirmed by the experimental results. The operation resulted in a deafness that was strictly confined to a very small region of the tonal scale (one or two tones in breadth); and the nature of the defect depended on the site of the operation in the fashion that the resonance theory demands. Also, if two holes were bored at different points, the animal displayed two such "tonal gaps."

Upton ⁽⁴³⁾ (following earlier and cruder experiments by Yoshii, Hoessli and others) has made use of a different method. Guinea pigs were continuously stimulated, for a period of 70 days, by a tone of 600 vibrations per second. At the end of this time, they were found to be extremely insensitive to sound of this frequency, although they still

responded in normal fashion to tones of 1,000 vibrations per second. This result supports the resonance theory; for, according to that theory, we should expect the long-continued vibrations to cause injury only in one restricted portion of the basilar membrane and its associated structures, namely in the portion that resonates to vibrations of the frequency 600.

These experiments seem to furnish a beautiful confirmation of the resonance theory. Nevertheless, some very interesting observations have recently been made by Wever and Bray⁽⁴⁷⁾ which fit in with the other type of theory. These investigators find that the action current of the auditory nerve is rhythmical in form, reproducing very exactly the amplitude and frequency of the wave motion acting on the cochlea. They laid bare the auditory nerve in a cat, placed one electrode on the nerve and another on the body of the animal, and connected them to an amplifying system and a telephone receiver. The rhythmical variations of electrical potential in the nerve then gave rise to an oscillatory current in the receiver, and an observer in a remote room heard in the receiver an accurate reproduction of the sound that was stimulating the animal's ear. This result has been corroborated by Rademakers and Bergansius, who have recorded the electrical responses of the nerve photographically, and by others.⁶ Wever and Bray have also obtained rhythmic action currents accompanying sound stimulation in rabbits, guinea pigs, rats,⁽⁴⁶⁾ and turtles.⁽⁴⁸⁾

Although animal experimentation furnishes data supporting both types of theory—the theory of resonance and the opposing theory that assumes a reproduction of the stimulus waves in the auditory nerve impulses—there is not necessarily any contradiction between these results. As

⁶ Mention should be made of the fact that there has been a good deal of controversy about the interpretation of the Wever-Bray effect; some writers doubt that it is really to be attributed to the auditory action currents.

Wever and Bray explicitly recognize, one may have a theory that embodies both principles. Troland had already suggested that such a synthetic theory is necessary if we are to explain all the phenomena of audition.

The problem of hearing in *fishes* has long been controversial.^(4, 44) The most thorough experiments on the responses of fishes to vibratory stimuli have recently been made by Stetter.⁽⁴¹⁾ This experimenter succeeded in training minnows and catfish to associate food with the vibrations transmitted to the water from sound sources in the outside air—whistles, bells, the human voice, and so on. The experiments succeeded equally well with blind and seeing animals. Vibrations having a frequency of several thousand per second were responded to; in the catfish, the upper limit was found to be about 13,000 per second. It was found that the weakest sound to which the fishes can respond is of the same order of magnitude as the least perceptible sound for the human subject.

Stetter also succeeded in training the fishes to discriminate between tones of different frequencies. (It was impossible, on the other hand, to establish a selection of one particular *intensity* when the frequency was held constant.) Only large differences of frequency, of the order of an octave, were usually discriminated; a few minnows succeeded in distinguishing between 288 and 341 vibrations per second—a difference of 53.

Like man, the minnow is capable of "tonal analysis." After being trained with a particular tone, the fish is still able to distinguish this particular frequency even when a number of other frequencies are sounded simultaneously.

In another respect, the fish behaves very differently from the human subject. In human hearing, two tones that are an octave apart, that is, have a frequency ratio of 2:1, sound very similar, and are sometimes confused with one another even by practiced musicians. The fish displays

no such confusion, but always discriminates tones more easily the greater their difference in frequency.

The fish's ear contains no structure analogous to the cochlea, but only a vestibule and semicircular canals (Figure 23). The vestibule consists of three chambers, the utricle, the saccule, and the lagena, each containing otoliths (small crystals of calcium carbonate). The otoliths are

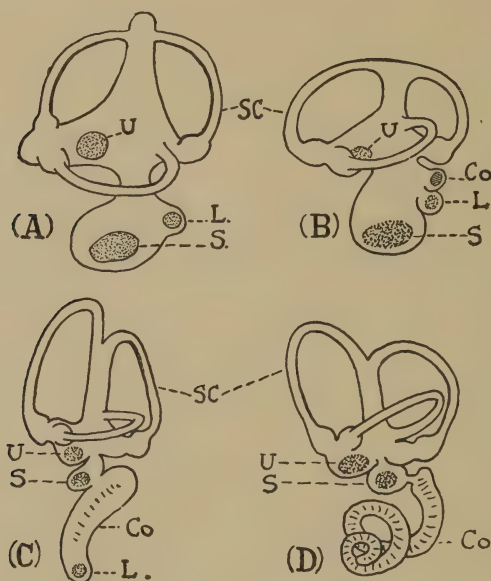


Fig. 23.—The inner ear. (A) of a fish; (B) of a frog; (C) of a bird; and (D) of a mammal. SC, semicircular canals; Co, cochlea; U, S, and L, otoliths of the utricle, saccule, and lagena. (After von Frisch.)

delicately balanced on fine hairs connected at their lower ends to sensory nerve endings. The otolith system in man seems to be concerned only with the control of bodily posture and equilibrium, but von Frisch and Stetter⁽³⁶⁾ have shown that the otoliths in the saccule and lagena of the minnow are concerned with *hearing*. Removal of these two structures causes no disturbance of equilibrium but

results in deafness. On the other hand, the removal of the utricle upsets equilibrium but has no effect on response to sound. Thus, these organs, though very similar in structure, have entirely different functions. Von Frisch and Stetter also inform us that the cutaneous receptors, in addition to the auditory receptors, come into play when the fish is stimulated by low frequencies.

The Wever-Bray effect, if it could be demonstrated in fishes, would make the facts of frequency discrimination intelligible. But the fish's capacity to "analyze" complex sounds raises a more difficult problem.

A number of *insects*, particularly insects such as cicadas, locusts, and crickets, which themselves emit sounds, possess on the thorax or leg a so-called tympanal organ, which is equipped with a drum-skin, like the human ear, and with receptor cells. The ingenious experiments of Regen ⁽⁴⁰⁾ have shown that this structure is a true organ of hearing. The female cricket, which is normally attracted to chirping males, ceases to respond to their chirping when her tympanal organ is removed. If the chirping of a male is transmitted by telephone from a distant room, normal females at once rush towards the instrument. In experiments with grasshoppers, Regen took advantage of the propensity of the male insects to chirp in alternation with one another. He found that a pair of males still displayed this alternation even though they were mounted on separate rubber balloons, so that no vibrations could be transmitted except by way of the air. But when the tympanal organ of one partner was removed, there was no longer any regular alternation. Whether the insects are capable of frequency discrimination is not known.

The study of hearing in fishes and insects, which possess auditory structures very different from those of man, offers an attractive field for future investigations.

The Chemical Senses

In human beings, we find two distinct chemical senses, smell and taste, which are subserved by different receptors, different nerve pathways, and different nervous centers. The sense of taste yields us four sensation qualities, sweet, salt, sour and bitter, and their intermediates. Through smell we obtain an enormous variety of sensations difficult to classify in terms of any simple system of elementary qualities.

In all vertebrates, the anatomist can identify two distinct systems of receptors, each with its separate nervous connections, which are entirely homologous with the smell and taste systems in man.⁽⁵¹⁾ We should expect these receptors to resemble the corresponding human receptors functionally as well as structurally. So far as experimental study has been carried, this expectation has been entirely confirmed.

The experiments of Strieck⁽⁵⁸⁾ on the behavior of fishes (minnows) towards chemical stimuli are of capital importance in this connection. Strieck first established the fact that the minnow can discriminate between chemical substances which for man arouse sweet, salt, sour, and bitter sensations, respectively. To begin with, the possibility of visual discrimination was excluded by blinding the fishes. A fish would then be fed for several days with bits of meat that had been soaked, for example, in acetic acid solution. A little later, the animal would be presented with bits of cotton wool saturated in a solution of sugar, salt, or quinine combined with meat juice (the chemical stimulus of the meat itself thus being a constant factor). Test experiments now showed that the animal had learned to associate the "sour" stimulus with food, and to distinguish it from the other three "tastes": if a bit of cotton wool soaked in acetic acid

solution was thrown into the aquarium, it was snapped at vigorously, but cotton wool soaked in any of the other three solutions provoked no response. In an analogous manner, Strieck was able to build up a selective response to a "sweet," "salt," or "bitter" solution.

Using three substances that have strong and characteristically dissimilar odors for man (skatol, cumarin, and artificial musk), Strieck succeeded in training minnows to exhibit selective response to one or another of these three "odors." The existence of two distinct senses, however, remained to be proved. Strieck therefore performed his next experiments on minnows from which the olfactory bulb of the brain had been removed. In such animals, it was found entirely impossible to establish a discrimination between "odors," while the discrimination of "tastes" was built up with the same ease as in intact minnows. It follows that the fish possesses two distinct chemical senses, resembling human smell and taste from the physiological as well as the anatomical standpoint.

The human receptors of smell are responsive only to gaseous substances, and those of taste to substances in dissolved or liquid form. In the fish, however, both types of receptor necessarily receive liquid stimulation, and yet the two senses are just as distinct physiologically as in land-dwelling vertebrates. The case of amphibians is particularly interesting in this connection; Matthes^(53,54) has shown that in salamanders (*Triton*), the same olfactory organ functions both in the air and under water.

The olfactory organ and its corresponding nervous structures are poorly developed in monkeys, apes, and men, as compared with animals like dogs, horses, mice, and rabbits, in which the sense of smell is of paramount biological importance. Yet the human olfactory organ, inferior as it is, presents us with a great complexity of different odor qualities, and its sensitivity is so great that we can detect odorous substances in quantities too minute to be registered by

the most refined methods of analytical chemistry. But common experience teaches us how much we are excelled by animals such as the dog in olfactory capacity. As yet, however, there has been little experimental analysis of olfaction in these animals.

Buytendijk ⁽⁵⁰⁾ has shown that dogs not only respond to odorous substances whose concentration is far too small to stimulate the human receptors, but that they have an extraordinary ability in "analyzing out" a given smell from a mixture of odors. The dog can also distinguish between the odors of certain chemically similar substances that have identical odors for the human subject.

Turning to the *invertebrates*, we find that two sorts of chemical receptors can be identified in certain of the insects, and that these may legitimately be called "smell" and "taste" receptors.

The olfactory receptors of insects are located on the antennæ. Von Frisch ⁽⁵¹⁾ has demonstrated that bees can be trained to associate odorous substances with food, and that this discrimination is lost when the antennæ are amputated. If, in advance of the operation, the insects are trained to make a color discrimination, the removal of the antennæ does not interfere with this reaction; thus, the result cannot be due to a general disturbance of behavior but is a specific defect of olfaction. The sense of smell in bees shows a number of striking and unanticipated parallelisms with that of man. In many cases, substances of different chemical composition that have similar odors for the human subject are also found to be equivalent stimuli for the bee. The least concentration of odorous substances that will give rise to discriminative behavior in training experiments with the bee is not greatly different from the odor threshold in man. The bee is superior to man, however, in its ability to analyze particular odors from a mixture of others—an ability that is of obvious biological advantage to the insect.

The gustatory receptors of the bee are located in the mouth cavity and in the tube-like proboscis. (Butterflies, as Minnich has shown,⁽⁵⁵⁾ possess taste organs on the legs.) According to von Frisch's experiments,⁽⁵²⁾ the bee distinguishes "sweet," "salt," "sour," and "bitter" substances, in analogy with man. But the bee differs from man in many of its reactions to "sweet" substances, which play such an important part in the insect's vital economy; for example, substances like saccharin, which have no nutritive value, do not seem to affect the "sweet" receptors of the bee.

Space Perception

Our knowledge of the means by which animals adjust themselves to the direction and distance of stimuli is at present rather meager.

The *visual appreciation of depth or distance* presents one interesting problem. In man, the perception of depth and solidity is primarily a binocular function. Köhler⁽⁶⁵⁾ has shown that binocular depth perception is also present in apes. The ape and the human being have eyes placed at the front of the head, so that a large part of the field of vision is simultaneously visible to both eyes. Many carnivorous mammals also enjoy a fairly large field of binocular vision, and it is to be presumed that this ensures the precise depth perception that they require in stalking and capturing prey. In herbivorous mammals, which belong among the "hunted" rather than the "hunters," a wide compass of vision is gained by lateral placement of the eyes, but the binocular field is then necessarily very small.⁽⁵⁾

However, Tschermak⁽⁵⁸⁾ and Rochon-Duvigneaud⁽⁶⁰⁾ have made careful measurements upon a number of vertebrates with lateral eyes, and in all cases it was discovered that there is at least a certain small binocular field. Herter⁽⁶²⁾ has experimentally demonstrated the existence of binocular depth perception in fishes. Many birds display

a remarkably accurate perception of depth; the adroit behavior of sea gulls in catching crumbs in the air is a striking example.

Russell ⁽⁶⁷⁾ has found that rats appreciate distance more accurately in binocular than in monocular vision, although the binocular factor is by no means all-important. Experimentation on animals would seem to offer a fruitful field for the investigation of the role of learning in depth perception. Observations made by Hamburger, ⁽⁶¹⁾ Bird, ⁽⁵⁹⁾ and others indicate that chicks that have been hatched in the dark are at once able to peck at grains with considerable accuracy; this furnishes clear evidence for the importance of a hereditary factor in the perception of distance.

Experimental studies on sound *localization* in animals have been made by Katz and his pupils. ^(60, 63, 64) It was found that dogs can localize sounds with remarkable accuracy. In the most favorable case, a sound coming from a direction that made an angle of only 51' with the median plane of the animal was distinguished from a median sound. It is probable that this localization depends primarily upon the slight difference in time of arrival of the sound at the two ears, as in human hearing. In man, the ears are much farther apart than in the dog, and the time differences are correspondingly greater; nevertheless, the best human subjects cannot distinguish the directions of sounds that differ by much less than 4°. An angle of 4° corresponds to a time difference of about six hundred-thousandths of a second for the human subject—a difference so small that it is very difficult to understand how it can be physiologically effective. But the minimal angle of 51' obtained with the dog represents a time difference amounting to only four millionths of a second. In cats and chickens, the minimal effective time difference is of the same order of magnitude.

Katz has found that human subjects can localize vibrating objects *tactually* by virtue of slight differences in the

stimulation of the two hands, and here again it appears that minute time differences play an essential role. It is probable that a similar principle operates in many animals; it is certain that the so-called "vibration sense," which displays so many analogies with the sense of hearing, is often an instrument of great biological significance.⁽⁶³⁾

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CHAPTER VII

Discrimination.

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ASSUME that you are one of a group of opossum-hunters in the foothills of the Great Smoky Mountains on a warm evening in November. The rain has ceased and the moon is just showing through the clouds. The dogs are unleashed and in a few minutes Lindy, the youngest dog, starts down through the thicket in full cry; but not a sound comes from the other two. "Lindy's jumped a rabbit," is the only comment. You walk along the ridge for a quarter of a mile or so, stopping occasionally to listen to the other dogs working the hollows on either side. Presently, Don gives a few excited yelps, to which are soon added the full-throated cries of old Lead. "Oh, boy! When Lead opens like that, the 'possum can't be far off." Lindy joins the others and the tongueing of all three dogs grows shorter and more frequent as the chase becomes hotter, until it suddenly changes to a perfect medley of high-pitched barks and yelps. "He's treed!"

In the foregoing illustration, one finds numerous suggestions that animals can react differently and discriminatively to complex stimulating conditions in their environments. Lindy distinguished between "animal-odor" and "no-animal-odor"; the older dogs displayed restraint to a rabbit odor; Don picked up another animal scent, announced his find, and began to follow the trail; and, finally, old Lead made known his recognition of a specific kind of scent, namely,

that of the opossum. Although these evidences of discrimination are well-nigh incontestable, the life situations in which they appear are so complex as to make impossible a satisfactory analysis. Therefore, before accepting them at their face value, one is forced to supplement them with more crucial evidence from simple but roughly comparable situations in the laboratory.

Using the term *discrimination* in a very broad sense, one may say that each time that an animal performs one of two alternative acts, it gives evidence that it can make at least a simple kind of discrimination and, therefore, that it has some basis for learning. The same idea, in its converse form, is well expressed by Dockeray when he says,

Let us suppose for the moment that the organism is not differentiated in any respect, that any and all stimuli act upon it in the same fashion and elicit only one, and always the same, response. Obviously, then, since differential response is not possible, only one unit of behavior could be exhibited. The organism could react by withdrawing from or approaching the stimulus, but it could not do both. If only one response is possible, and it makes no difference what kind of, or how many, stimuli bring out this one response, then modifiability of behavior would be totally absent. We would say, therefore, that the animal lacked sensory discrimination and could not learn.⁽³⁾

Chapter VI, with its emphasis on sensory motor mechanism, has already prepared us to accept evidence of exceedingly delicate discrimination among the lower as well as the higher animals. Those reactions, however, were more purely of the sensory character. In this chapter, we shall go somewhat beyond the sensorimotor level in order to ascertain whether there are still other forms of discriminative responses: in particular, discriminations that are based on "relationships" and "qualities" of the total situation that may not be apparent in the objective stimuli. Taking our cue from man, we should expect to find such instances in complex situations offering opportunity for generalization, abstraction, concept formation, insight reaction, and so

forth—in short, wherever adjustments of the more complex character are called into play. Therefore, the present chapter will be concerned not only with the more purely sensory forms of discrimination in animals, but also, to some degree, with investigations pertaining to concept formation, abstraction, relational “thinking,” insight situations, and so on. So far as possible, we shall choose examples from among those studies that best reveal the animal’s methods of work as well as the exact nature of responses used as indicators of discrimination.

Behavioral Aspects of Discrimination

Assuming that an animal has the sensory, nervous, and motor structures necessary to perfect a given discrimination, just how are we to decide when a discrimination is made, on what sensory cue it is based, and to what extent various sense modalities are involved?

In the lower animals, we are deprived of language responses and have to depend for our cues upon gross movements of muscle groups. The question then becomes, “What movements can be used as indicators of changes that are taking place in the animal during the learning situation? Under what conditions are these indicators valid?”

Stagner⁽²²⁾ has listed four different types of responses that may be used to indicate that an animal is influenced by the stimulus:

- (1) A regular reaction whenever the stimulus is presented (tropistic responses, respiration changes, the psycho-galvanic reflex);
- (2) the natural differential response, involving a multiple-choice situation in which the individual may express a preference;
- (3) the method of acquired response, as exemplified by the conditioned-reflex method; and
- (4) the method of acquired differential response, in which the animal is presented with an asymmetrical situation to which he must react. The last includes the Yerkes apparatus and its variants, which include essentially a uniform stimulating situation which is asymmetrical with respect to a single detail.

If now we consider a well-known type of experiment in which evidence for a discriminative reaction is being sought, some idea of the intricacies of the discrimination method in animal research is revealed. Suppose that one desires to have white rats form a *brightness*-discrimination habit, and proposes to use the Yerkes apparatus,⁽³²⁾ in which the animals will be required to turn into an alley on the side of the brighter of two lights in order to obtain food or to avoid punishment. What factors must be controlled in order to assume that the animals are discriminating on the basis of the brightness of the stimulus-objects and that alone?

In the first place, we should remember that, in scientific experiments, the general rule is to control or hold constant all of the possible cues but one (brightness in this case), and then to vary that cue systematically. In the present experiment, we must make sure that the rats cannot respond correctly to the sound of the apparatus; to the odor or smell of one pathway as opposed to the other; to the tactile or thermal qualities of the stimuli; to special handling cues given by the experimenter; to proprioceptive stimulation; or to position habits (always running to the right, and so on).^{*} If we are quite sure that the rats are not using any of these cues, and if totally blind rats cannot learn the problem, there is good reason to believe that the essential stimulus is visual in nature. Still one does not know just what visual stimulus is being used. To guarantee that the animals are responding only to brightness, one must control shadows and make the stimulus-objects of equal size and shape and place them in the same positions with respect to background, distance above the floor, and the like. Now, assuming that the rats have formed the discrimination habit, with each of the foregoing factors controlled, we should still make one last check: we should make the stimulus-objects almost equal in brightness (of no discernible brightness difference for the mammalian eye) and continue the tests. If the rats can no longer respond accurately but

show hesitation and become confused, we may assume that their reactions just before the final crucial test were made on the basis of a brightness difference of the stimulus-objects. Even yet, however, our task as a whole has not been finished. We should now proceed to inquire as to which stimulus-objects the rats responded to and as to the relative importance of absolute brightness factors versus relative brightness of the two stimuli. Also, if certain individuals failed to form the discrimination habit, we should seek the cause of their failure—that is, whether it should be attributed to stupidity of the animals, to difficulty of the task, or to inadequacy of the training methods.

These are a few of the problems that must be considered in so simple a problem as brightness discrimination, and the number increases as more complex discriminations are studied. It is probable that the difficulties encountered in the control of conditions account for the dearth of worthwhile experimental data on some of the senses.

Vision

Since by far the greater part of the experimental work on discrimination by animals has been done in the field of vision, we shall start with that sensory modality. The experiments may be divided into at least five groups, dealing with the discrimination of brightness, size, form, color, and distance, respectively.

In 1907, Yerkes and Watson were asked by a committee of the American Psychological Association on the standardizing of procedure in experimental tests to devise “a standard procedure for testing color vision in animals.”⁽³²⁾ Four years later, their report was published. The scope of their investigation had been broadened to include methods of studying the perception of light, size, form, and distance as well as color. Yerkes had been given charge of the general direction of the work and was chiefly responsible for the

method and apparatus recommended for the study of light vision. These bear many resemblances to the apparatus and method he had used earlier in his study "The Dancing Mouse."⁽³¹⁾ Modifications of his apparatus were influential in shaping the experimentation of the next twenty years, and it is only recently that any significant changes have been made.

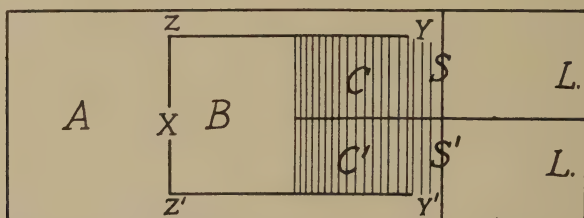


Fig. 24.—Floor plan of the Yerkes-type discrimination apparatus. *A* is the combination food and starting box. A rat released here goes through the door *x* into the discrimination chamber, *B*, from which it views the stimuli (*S* and *S'*) from in front of the electric grills. The partition and grill force the rat to make its discrimination from in front of the alleys *C* and *C'*. If the rat reacts correctly, it goes toward the positive stimulus, pushes through doors *y* or *y'* and *z* or *z'*, and receives food in *A*. In case of an incorrect choice, the door *z* or *z'* remains closed and the rat is forced to go to *A* by the other path.

The essential features of the Yerkes apparatus are shown in Figure 24. It consists of a discrimination chamber from which the animal can look across an electric grill at two photic stimuli on either side of a partition. If the animal makes a correct response, it crosses the grill in front of the positive stimulus-object, turns to the right or left as the occasion demands, pushes through a door, runs toward the front of the box, and finally pushes through another door into the food compartment. In case of an incorrect response, the door into the food compartment remains closed and the animal is given an electric shock and is forced to return to the discrimination chamber. If the positive stimulus is on the right for the first trial and the animal has

gone to the left, it is shocked at once. The next time that it is put into the apparatus, there is a tendency for it to avoid the side on which it has just been punished. In the meantime, the position of the positive stimulus may have been changed (it is necessary to change the position according to a chance order so that the rat does not learn to go to the same side every trial) so that the rat is now shocked on the right side of the apparatus. Thereafter, the animal will run to the front of the grill, go from one side of the partition to the other, and finally dash down one alley. Even though the animal makes a correct discrimination, as yet there may be no close association of the food received after this run with the stimulus-object seen from the discrimination chamber. The first behavioral evidence for a discrimination is manifested when the animal runs back and forth in front of the grill with its nose pointed toward the stimuli "as if" it were looking at them. But the actual runs across the grill toward the stimuli are the only data upon which a criterion of discrimination can be based.

When human subjects agree in seventy-five per cent of the cases on a problem limited to two choices, we have said that there is evidence of a discrimination. However, in work with animals, an individual accuracy of ninety per cent or better must be obtained in order to be free from criticism, despite the fact that it is more difficult to direct the attention of an animal toward a critical point than it is to do so with man.

Brightness discrimination.—Using modifications of the Yerkes-Watson apparatus, various investigators have been able to establish discriminations between a standard light and a variable (brighter or darker than the standard) in fish, mice, white rats, guinea pigs, rabbits, chickens, certain birds, raccoons, porcupines, cattle, dogs, and monkeys. The training period needed to establish the discrimination has varied from 50 to 500 trials, depending upon the animals used. In the few experiments that have been undertaken

for the purpose of establishing differential brightness thresholds, we find threshold values ranging from ten to eighty per cent of the standard brightness. Turtles, pigmented rats, and cats have established differential reactions between two brightnesses when other types of discrimination apparatus were used. There seems to be pretty general agreement that most animals can distinguish between different brightnesses. Although this is one of the easiest discriminations to establish, it remains for future research to determine exactly how small brightness differences can be made before they cease to be discriminable by various animals. (See Chapter VI for further data on this point. For a good bibliography and résumé of material on visual discrimination see reference 22 by Stagner.)

Size discrimination. Using the Yerkes-Watson apparatus and method, it has been possible to obtain size discriminations in most of the animals studied. In this case, however, the problem is complicated because the larger stimulus area also has a greater total luminosity. It has been suggested that some of the size discriminations were in reality discriminations of the total amount of light given off. Where the differential threshold has been investigated, the value obtained has been about twenty per cent of the standard.

Form discrimination.—Although the Yerkes-Watson apparatus is satisfactory for brightness- and size-discrimination experiments, investigators have not been able to establish "form discrimination" with it in the various animals used. By "form discrimination" we mean a differential reaction to dissimilar geometrical figures of equal area and brightness. After several attempts had ended with failure, the known anatomical data concerning the eyes of the various animals tested were interpreted in a way to make them conform to the experimental findings. Since the published evidence from both sources corroborated one another, there grew up a fairly general acceptance of the view that

animals below primates cannot distinguish between different geometrical figures. Much of this early work had been instigated to learn whether the animals might have "images" or some other substitute for "ideas." When the form-discrimination experiments designed to demonstrate their presence gave negative results, the question of the use of symbolic cues was also dropped.

In 1926, Fields modified the original Yerkes box so that (1) the animals could see both figures simultaneously from any point in the discrimination chamber, (2) the animals ran under the forms to be discriminated and continued in a straight line from the starting point to the food box, (3) the reward of food was given immediately after the correct discriminative response, and (4) detention after an incorrect choice with no food until the next correct run was substituted for the electric shock. Under these conditions, he obtained positive discrimination of geometrical figures of equal area and brightness.⁽⁴⁾ Since then, Lashley⁽¹⁶⁾ has secured form discrimination in rats by a method which requires that the rats jump across a gap to the form (see Figure 25). If they jump to the correct form, the card on which it is placed falls down and the rat at once secures food. If it jumps against the incorrect form, the card remains in place and the rat bumps its nose and falls about two feet into an apron, from which it is lifted to the jumping stand for the next jump. The positive results obtained by Fields and Lashley demonstrate that failure to learn to discriminate in the earlier experiments was not due to the rat's inability to discriminate the forms, but to its inability to master other details of a complicated situation.

Lashley then undertook an investigation of the structure and image-forming power of the rat's eye and found that it has fairly effective detail vision with an acuity from about one fiftieth to one twenty-fifth that of man, and an ability to discriminate complicated patterns above this threshold. Anatomically, the rat's eye represents a fairly efficient opti-

cal system conforming in its possibilities to the actual findings in recent tests of visual discrimination.⁽¹⁷⁾ Thus, the earlier interpretations of anatomical data have also been reversed.

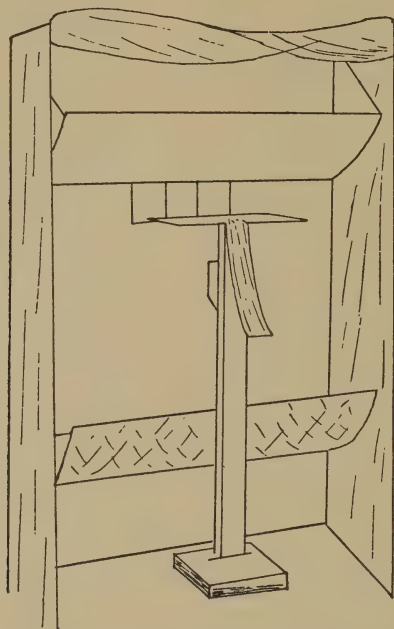
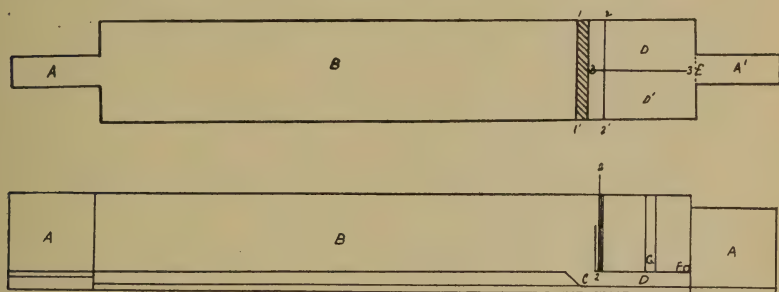


Fig. 25.—Modification of Lashley's two-choice jumping-type discrimination apparatus (after Fields). The screen is a three-ply wood panel 4 feet by 6 feet. The two openings in which the forms are exposed are 6 inches square, separated by $4\frac{1}{2}$ inches, and are 4 feet above the floor. There is a $3\frac{1}{2}$ -foot drop from the bottom of these openings to the apron below. The metal flange above these holes extends forward and upward for 18 inches across the complete width of the screen. The food platform at the back of the holes (not shown) is 15 inches by 21 inches, with raised edges to prevent the rat or food from sliding off.

The top of the jumping platform is 10 inches by 18 inches, with the long side facing the holes in the screen. A wire ladder 3 inches by 20 inches was hung from the middle of the platform at an 85° -angle. The light box was 3 inches by 5 inches, placed on the stem $4\frac{1}{2}$ inches beneath the surface of the jumping stand so that the rat's shadow would not fall on the figures as he stretched out toward them.

Using a modification of his earlier form-discrimination apparatus for rats (see Figures 26 and 27), Fields combined five of these units in serial fashion (similar to Stone's⁽²³⁾ use of the multiple-light-discrimination apparatus) and obtained positive figure discrimination with raccoons.⁽⁸⁾ These data substantiate the findings of Cole on figure discrimination in the raccoon reported in 1907.⁽²⁾



Figs. 26 and 27.—Modification of the running-type discrimination apparatus (after Fields). *A* and *A'* are interchangeable starting and food boxes; *B* is the large upper discrimination chamber; *C* is the lower floor level; *D* and *D'* are two dark chambers under the light box separated by the partition 3-3' but opening into the food box *A'* by the door at *E*. The partition under the light chamber extends forward to the stop at 1-1' and is of the same level as the floor of *B*. The form-board is at 2-2' with a pane of clear glass immediately in front of it, and two opal flashed glass panes back of it. Between the 25-watt lamp at *F* and the opal flashed glass were placed 12 thicknesses of cheese cloth (*G*), used to cut down and diffuse the light.

The ability to discriminate between geometrical figures has been studied in still other ways with certain birds, chickens, cats, dogs, and monkeys. Food was placed in two containers differing in shape and the animals taught to eat from a particular shape: with birds, the grain on the negative figure was soaked in quinine and they soon learned to avoid it. Other variations of the same technique are the presenting of food itself cut into different shapes. Either the negative pieces (squares) are glued fast to the floor, or

quinine is placed on the back or under side, while the positive pieces (circles) are free. After preliminary training of the animals, in the critical test situations food in both shapes and perfectly free is scattered around. Now the animals eat only circles although they would not be punished for eating the squares.

The principal objection, from the experimenter's standpoint, to all of the problems on visual discrimination is the extremely long training period necessary to establish the initial responses. Lashley's "jumping" apparatus is an improvement over any of the existing "running" types of apparatus; but even with this apparatus, when complicated problems are under investigation, the routine of training is too long.

Fields has recently reported a modification of this apparatus in which five different figures can be exposed simultaneously and which provides a number of controls not possible with the usual two-choice apparatus.⁽⁷⁾ With this apparatus, rats learn problems in approximately one half the number of trials required on the two-choice apparatus (see Figure 28). This apparatus makes possible the investigation of a larger number of control or experimental problems during the lifetime of the animal.

Color discrimination.—Watson's principal contribution to the monograph "Methods of Studying Vision in Animals" ⁽³²⁾ consisted of the apparatus and method designed for the study of color vision. The complexity and expense incident to its construction have militated against its use in many laboratories, and although the use of spectral light is to be desired, it has been replaced in most instances with colored paper, paint, and colored lights (in a few instances, color filters were used). The method that has been most productive of good work on color vision in animals is one that requires them to pick out a given color from a whole series of grays. If the animal's discrimination depends upon brightness, then there will be some point in the gray

series that will match the color, and the animal's reaction at that point will be reduced to chance accuracy.

In experiments with fish, various species have been trained to snap at food when it is held by certain colored forceps and not to snap when the food is held in forceps of another color. Reeves ⁽²⁰⁾ adapted the Yerkes-Watson type of apparatus to use with fish, and found that sunfish

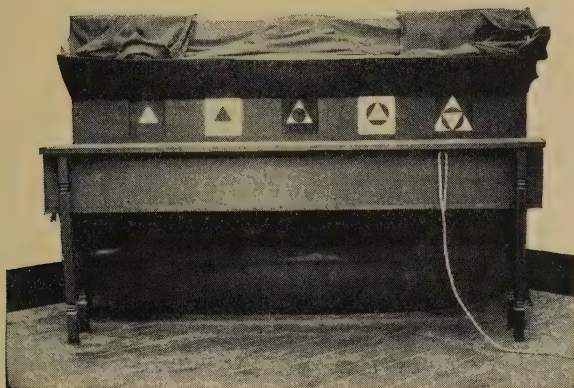


Fig. 28.—Fields' multiple-type jumping discrimination apparatus. The screen is a panel of three-ply wood 3 feet by 6 feet. Each of the five openings is 6 inches square, and all of the openings are separated from one another by a 6-inch space. The metal flange above the holes is 12 inches wide. The jumping platform is 8 inches wide and 6 feet long. The top is on a level with the bottom of the apertures (30 inches above the floor) and can never be moved more than $9\frac{1}{2}$ inches from the forms because of the wall back of it. The entire apparatus is carefully screened. Rats learn to jump to all of the designs shown in the apparatus. When only two designs are used in the multiple apparatus, the rats still learn more rapidly than on the two-choice apparatus shown in Fig. 25. (See reference No. 6 for illustrations of the stimuli used in various visual-discrimination experiments.)

and dace could make the discrimination of spectral colors even after changes in the relative intensity of the two lights. There is very little evidence of color discrimination in reptiles and amphibia, and no good evidence that mice, rats, guinea pigs, dogs, cats, squirrels, porcupines, rabbits,

or cattle can discriminate colors from a gray of the same brightness when secondary cues from the experimenter are absent. In several of these animals, the absence of color vision has been associated with the lack of cones in the retina.

Most of the positive data on color discrimination have been obtained from birds—either chickens or pigeons—and from monkeys or apes. In all of these animals, cones have been found in the retina. Lashley,⁽¹⁵⁾ using spectral stimuli, reports that after chickens were trained to react to colors, the association with wave length was dominant even when the brightness values of the stimuli were so greatly different as to call out the brightness preference in untrained birds. In studies with monkeys,⁽²²⁾ there has been introduced a new method in which the animal is required to match one colored object with another of the same color. This procedure gives results indicative of color vision.

Responses to Relative versus Absolute Differences in the Stimuli

It has been known for some time that in the ordinary discrimination problem in which paired visual stimuli are presented simultaneously, the animal may respond, as a result of training, not to the absolute qualities of the positive stimulus but to the relative difference between the two members of the pair. The common example is size discrimination. If animals have been trained to go to the larger of two figures (three- and four-inch squares), then when a four-inch figure and a five-inch figure are exposed simultaneously, they immediately go to the five-inch square although previous responses have been made to the four-inch figure. Kinnaman⁽¹³⁾ noted, in 1902, that monkeys responded to the relative rather than the absolute brightness when trained to get food from one of two glasses, one of which was covered by a light gray and the other by

a dark gray paper. If, in the training series, the positive response was made to the lighter paper, when two new grays of unequal brightness were presented, the monkeys at once selected the lighter gray. Similar responses to "relations" that involve visual stimuli have been obtained from fish, turtles, chickens, crows, rabbits, guinea pigs, rats, raccoons, and monkeys. Monkeys have demonstrated the same type of behavior in response to temporal intervals that are bounded by an auditory stimulus.

That an animal may respond to absolute stimuli has been shown by Warden and Rowley⁽²⁷⁾ in an experiment in which they trained one ringdove always to go to a particular gray regardless of whether or not it was the lighter or darker of the pair. However, the training period consisting of 1,000 trials was about double that which would have been expected had the bird been trained to respond to the "relative brightness."

Rats that have been trained to jump to a triangle with its apex up when it is presented in combination with a circle of equal area, will jump to the triangle when it is shown for the first time with other geometrical figures. But if the triangle is turned upside-down and exposed with the circle or other new figures, the rats will not jump to it; indicating that they had been responding to a particular position of the triangle. Fields⁽⁶⁾ gave a group of eleven white rats over 40,000 trials with eighty different stimulus-combinations and found that they could establish a positive response to either white or black triangles in many different positions. These rats eventually jumped to a triangular configuration of three small circles when presented with vertical or horizontal patterns of three circles of the same size. These data indicate that white rats may respond to "relationships" and "qualities" inherent in a stimulus-pattern.

Distance discrimination.—Although no one has been able to demonstrate the existence of a specialized sense organ

for the reception of distance cues, there is some evidence to show that distance is perceived through visual stimuli. In experiments with rats having normal vision, it has been shown that they gauge the force of their jumps from one platform to another by visual perception of the distance separating the two platforms.⁽³⁵⁾ Blind rats will not jump. Animals with portions of the brain destroyed may jump in the right direction; but if they have been accustomed to jumping 40 inches, and the stand is moved closer (20 inches), they go completely over it.

Yerkes⁽³⁰⁾ put different species of turtles on a board raised above the water of an aquarium. He found that the water-living species jumped off the board at any height, although unwillingly at 180 centimeters. The water-land turtles were slower in jumping, and the land species would not jump at 180 centimeters.

Observational studies (not controlled experimental studies) have shown that some monkeys could estimate distance to within two or three centimeters, when reaching for food placed outside the cage was used as a measure. If the food was a few centimeters farther away than they could reach, they did not try to get it. It must be true that a gibbon possesses accurate distance discrimination, because it can seize moving objects while it is in the air, midway between two branches.

Auditory Discrimination

The difficulty encountered in confining an auditory stimulus to a particular spatial point has made the use of an apparatus similar to that employed in the investigation of vision almost valueless in studies of auditory discrimination. For that reason, although there are many studies of auditory sensitivity in animals, using various training methods, we have very few reports of discriminations established where the two auditory stimuli were presented

simultaneously. This temporal factor in the presentation of the stimuli may be a complicating factor about equal in importance to the turns encountered in the original Yerkes apparatus.

The first studies of hearing were concerned with the animal's ability to distinguish a noise from silence. The earliest qualitative studies consisted of the observation of bodily movements in response to sounds. Evidences of hearing were such responses as pricking the ears and awakening from sleep. Pigs, cows, and horses were observed to respond to both high and low tones; mice, rabbits, and hedgehogs gave responses only to high tones, while cats and dogs scarcely noticed them. There is some evidence that certain fish can hear in their rising to the top of the water to be fed when a familiar noise is produced. However, these responses are not comparable to the discriminations obtained with variants of the Yerkes apparatus wherein the animals were required to respond in a definite manner to the positive and the negative stimuli.

Hunter used a T-shaped discrimination box in a long series of experiments with white rats in which the animals were trained to turn to one side when an auditory stimulus was given and to the other if it was lacking. Noises and whistles were effective in establishing the habit, but when a pure tone (from a tuning fork) was used, his animals could not make a discrimination. He then tried to train rats to make a discrimination on the basis of tone by gradually reducing the noise factor in a compound stimulus of noise and tone, but was not successful.⁽¹²⁾ However, Muenzinger and Gentry succeeded in training rats in a Y-shaped discrimination box to turn to the right when a diffuse tone was sounded and to the left when there was no sound, and to discriminate a tone-filled alley (an oscillator in the end of the alley was the tone source) and one comparatively silent.⁽¹⁹⁾ Thuma, working with rats, has reported a similar discrimination of relatively pure tones of

high intensity.⁽²⁵⁾ Thus, the most recent, and perhaps the best controlled, experiments, indicate that the white rat can discriminate pure tones with a frequency of from 1,000 to 4,000 vibrations per second.

When we turn to other training methods for the study of auditory sensitivity, we find that Anrep, using the Pavlovian conditioned-response method, was able to establish a discrimination between sounds of 637.5 and 680 vibrations per second in dogs.⁽¹⁾ Other investigators have demonstrated relatively constant changes in either blood pressure, cardiac rhythm, or respiratory rhythm in frogs, rats, guinea pigs, rabbits, cats, and dogs in response to auditory stimuli.⁽¹¹⁾ Wever has reported that action currents in the auditory nerves of various animals correspond to the stimulating tone. For turtles, the range of frequencies was from 120 to 1,000 vibrations per second, and for rats, rabbits, guinea pigs, and cats, 105 to 5,200 per second.⁽²⁹⁾ In but few of these studies was a differential reaction (such as turning to the right for 512 vibrations per second and to the left for 480 vibrations, and so on) to various stimuli demonstrated.

Olfactory Discrimination

In Liggett's monograph on an experimental study of olfactory sensitivity of the white rat, we find the following statement: "None of the experiments with rats have been designed to test olfactory ability, but rather various experimental results have been said to be influenced by olfaction."⁽¹⁸⁾ He repeated Vincent's earlier work on odor trails in a maze (alternate strips of beef extract and cream cheese in the true pathway being used), and found no significant differences between the control group and the odor-trail group. The behavior of his animals gave no information regarding their sensitivity to the odor trail. Liggett then built a T-shaped discrimination box and secured only

negative results with oil of bergamot, roquefort cheese, carbon bisulphide, and oil of anise. Three of his rats learned to discriminate between amyl acetate and oil of anise. In a Yerkes box, some rats learned to discriminate between oil of sassafras and violet perfume, and between amyl acetate and no odor. These discriminations were too unstable to allow control tests to be made. He concluded that the rat could be trained to react to odor stimuli, but that such discriminations were hard to set up, were very unstable, and that the rat was less easily influenced by olfactory than by visual and auditory stimuli.

Liggett reported a supplementary experiment by Spieth in which cheese was recovered by rats when it was buried in sawdust, a method by which vision and kinæsthesia were excluded as cues. When cork the same size as the cheese was buried in place of the food, the rats, excepting a few cases, did not locate the cork. Swann has extended this method by requiring his animals to dig through odorized shavings to reach food. He reports that his rats can discriminate (1) between butyric acid and a disinfectant; (2) "Trail Scent" (a commercial paste supposed to attract animals to traps) and gasoline; and (3) anise and a disinfectant. Liggett reported in his study that possibly his animals were reacting to cutaneous components of the situation. Perhaps the same criticism may be directed against Swann's results.

About the only animal for which we have positive evidence of olfactory discrimination is the dog. It has been found sensitive to many odors (flower perfumes as well as food odors) and has perfected differential reactions to them under several different types of training methods. Evidence of olfactory sensitivity has been noted in fishes and amphibia, but the discrimination method was not used to establish it. It has not been conclusively shown that birds can smell, although there seems to be some justification for crediting the turkey buzzard with this sense.

Gustatory Discrimination

Some light has been thrown on the question of gustatory discrimination by the recent studies of food preferences. Although this sense modality has not received much attention in the experimental laboratory, it has generally been accepted that animals can differentiate gustatory qualities of substances, and that their subsequent activity may be modified on the basis of this experience.

The "salt hunger" of animals is a case in point. In earlier periods, game trails leading to "salt licks" were prominent, and animals traveled many miles to secure the substance. It is to be noted that they were able to distinguish between the salt springs and the iron and sulphur springs. Examples are on record where animals have eaten earth which contained minerals necessary to their health. Dr. C. R. Carpenter has photographed a cave that has been constructed as the result of the wild hogs of the Barro Colorado Island eating out this particular layer of earth in the side of a hill.

In various feeding experiments in which animals were unrestricted in their choice of quantities and kinds of food, they have shown ability to select a diet adequate to their bodily needs. This is especially true of hogs and cattle. But the inference that this is indicative of gustatory discrimination is complicated by Young's report ⁽³⁴⁾ of an experiment by Price in which chickens were allowed to choose from three kinds of butter:

... (1) butter high in vitamins A and D, (2) butter high in A but low in D, and (3) butter low in both A and D. He found that chickens ate the greatest amount of the first food, which is of course the most adequate to meet their bodily needs. He does not know how the foods were discriminated, for to the human observer the flavor (taste) and odor gave no clue, and the containers were of the same size and shape and shifted in position indiscriminately.

Of course, we can say that chickens and man may not have the same type of sense organs and that they might not be expected to taste in the same manner; but the fact that this behavior was relatively constant leads one to conclude that a discrimination was made, even though we are not sure that it was gustatory in origin. Bayer made a behavioral study of the food preferences of the hen and found that different kinds of grain arrange themselves into preferential series. Corn (maize) was most preferred and rye least; between these extremes were wheat, barley, oats, and rice. Fischel, in a study of memory as shown by food seeking in which he utilized the food preferences of animals, reported that the porcupine preferred white to rye bread, that goats preferred rye bread to several other foods tested, that mice preferred shelled to unshelled oats, and so forth.⁽³⁴⁾

Young has devised an apparatus for the experimental control and study of food preferences in the white rat. In the center of a feeding table is an opening within which two test foods can be presented simultaneously. Foods are presented in glass tubes, leveled off to the top of the tubes, and the tubes are interchanged in position on alternate trials. The floor of the table is made of quarter-inch wire mesh; hence the food spilled by the rat immediately falls out of reach. The test foods used were: fresh milk standardized at 4-per-cent butter fat; pure butter fat; cane sugar, granulated and extra fine; white wheat flour; whole-wheat powder; and dried whole-milk powder. Young says,

When rats are given a preference test with two foods, individual differences in relative preference at first appear. Upon repetition of the test, one food is selected by the group with relatively greater and the other with relatively less frequency. The gradual change toward one test food and away from the other has been called a preferential trend. . . . Preferential trends when graphically represented resemble learning curves. It is fair to assume that the curves show learning, for when a rat is given a pair of foods, he must learn to

discriminate between them on the basis of taste, smell, or appearance, or upon some other basis.⁽³³⁾

We have no definite evidence that this discrimination is gustatory, but whether it is or not could easily be ascertained by ruling out vision (by blinding the rats or by testing them in the dark), by choosing food substances that are not odorous and that are of the same texture, solubility, and so on. A discrimination between salt and sugar might thus be made to depend upon taste, and the acuity of the sense might be studied by presenting these substances in different proportions along with a constant standard (100 per-cent sugar presented with mixtures ranging from 90 per-cent sugar and 10 per-cent salt down to 90 per-cent salt and 10 per-cent sugar, and so forth).

The fact that the presence of quinine on food will cause an animal to cease eating it is good evidence of gustatory discrimination. There is some evidence, however, that animals with a well-developed olfactory sense may even scent quinine sulphate when it is on the underside of the food. Certain fishes and amphibia have been taught to discriminate meat juice when it is mixed with the different chemicals that give rise in man to the four elementary tastes, but this work has not been extended to include the higher species of animals.

At present, the general consensus of opinion seems to coincide with the view that animals could make gustatory discriminations in controlled tests if given an opportunity, but this opinion should be supported by more experimental data.

Cutaneous Discrimination

Most of our information concerning cutaneous discrimination has been incidental to the study of other problems. Unless these cues are controlled in other types of discrimination work, the criticism may be raised that the animals may not be responding to visual stimuli (or the sense mo-

dality under investigation) but to the roughness of the floor or sides of one part of the apparatus as opposed to the smoothness of other portions. The question of thermal discrimination has not been studied, but it is known that rats swim in water with a temperature of 10 degrees Centigrade in a manner different from that used in water of 40 degrees Centigrade.

In 1911, Vincent ⁽²⁶⁾ reported on tactual discrimination in an article in which the function of the vibrissæ in the behavior of the white rat was investigated. She constructed an apparatus with three runways each four inches wide and with sides five inches high. The two sides of one alley were made of vertical corrugated linings, and the other two alleys had plain, smooth linings. The position of the corrugated alley was changed from time to time and the rats were supposed to choose this pathway to the exclusion of the others. The rats used were classed as normal, anosmic, blind, and with the infraorbital branch of the fifth nerve cut, the first two groups containing some animals with and some without the vibrissæ. The results show that the tactile hairs play an important part in the discrimination of surfaces. Not only is the number of trials in learning greatly increased by their removal, but the time is greatly lengthened. The work also seemed to show that the power of discrimination that remained after the removal of the vibrissæ lay in the very sensitive nose, since the blind rats and the anosmic rats could make the discrimination, while rats with insensitive noses and no vibrissæ failed. It was also demonstrated that a rat with vibrissæ cut on the right side would keep close to the left side of a maze alley, and that one with the left vibrissæ cut would follow the right side. There was a tendency for the rats to rub against the sides of the runways with their bodies and there was a possibility that they could make the discrimination between the smooth and corrugated alleys from cutaneous cues received in that manner.

Fields trained normal rats to crawl through variously shaped apertures and found that after they were blinded the accuracy of the reaction did not decrease to any appreciable extent.⁽⁴⁾ It is evident that kinæsthetic cues may have been present in addition to cutaneous ones, for the muscular reactions in crawling through a triangle on its base are not the same as when the triangle is placed on its apex, the lowest part of the figure in the two cases being equidistant from the floor.

At the present time, Mr. Clifton Moore (in the Maryville College laboratory), using a simple elevated Y-maze with the floors of the Y covered with sandpaper of different degrees of coarseness (the positive path being covered with No. 2 coarse, and the negative path with No. 00, fine paper), is obtaining some evidence that white rats can make a discrimination on the basis of cutaneous stimulation of their feet. The rats pause at the Y, putting the forefeet alternately on the two paths, or one foot on each path, and go through the same type of behavior that characterizes a discrimination in other problems. It should be comparatively easy, in the same way, to establish differential reactions to temperature and then to determine the differential thresholds.

Proprioceptive Discrimination

We have some evidence for a proprioceptive sensitivity in the geotropic responses of animals. These were first investigated by the discrimination method by Dashiell and Helms.⁽²¹⁾ They showed that some white rats could learn to modify their direction of locomotion in terms of the inclination of the paths from the horizontal. Ruch⁽²¹⁾ designed a triple-unit, Y-shaped discrimination apparatus wherein the branches of the Y varied with respect to the degrees of slope upward, and found that a 10-degree difference could be discriminated accurately after a com-

paratively short training period. He used blind animals in order to control visual cues. After some additional training, he investigated the differential thresholds of twenty-three rats, and reported that 96 per cent discriminated an inclination difference of three degrees, 61 per cent discriminated a two degrees' difference, and 13 per cent discriminated a difference of one degree. The animals that had made the one-degree discrimination responded according to a chance expectancy when there was no difference in the inclination of the alleys. Miss Ruth Tinsley (in the Stanford University laboratory), using a more refined apparatus, has demonstrated that cats can make a discrimination of three degrees of inclination.

Klüver⁽¹⁴⁾ has devised a "pull-in" technique, for use with monkeys, by means of which he has tested weight discrimination. Two boxes that look alike are placed outside of the cage, strings are attached to them, and different weights are placed inside. The monkeys soon learned which box to pull in order to get food. This technique may be used for the investigation of other senses and is adapted for use with other animals, notably raccoons.

Directional Sense

The stories of cats and dogs that have been moved with their owners some hundreds of miles to a new home and who a few weeks later reappeared in their old surroundings have given rise to the belief that they (and animals in general) must have some sort of a sense of direction. No one has been able to isolate this sense, but various theories about it have developed. Gundlach tested some of these in a recent experiment with

a maze constructed in the shape of a plus sign, having an exit to the north and entrances from the east, south and west, and so arranged that, if an animal did not know at which entrance it was introduced, it could not solve the maze on the basis of normal sight, hearing, smell,

touch, or kinæsthesia. The only constant factor was that the exit was always to the north, which was also the direction of food, the nest, and, in the case of the homing pigeons, of mate and young.

The maze should be soluble by any creature that has either (1) a 'homing instinct' which acts as a guide rather than as an urge, (2) a 'sense of direction,' (3) some 'magnetic' sense, (4) some subtle means of recording the turns of the outward path, or (5) some other type of unknown sensitivity that is activated by a peculiar emanation from the goal or nest. Three cats, two homing pigeons, and one tumbler pigeon were practiced upon the maze for more than 85 days each. The animals did not learn to solve the maze, and gave no indication that they could had practice continued. This evidence stands very conclusively against all of the five mentioned 'explanations' of homing, at least with respect to vertebrates.⁽⁹⁾

Warner⁽²⁸⁾ has reviewed the literature on homing in birds and finds more evidence for a "learning" theory of homing than for any other. Schneider believes that pigeons gradually acquire a knowledge of the topography immediately around their cote and that they then extend their knowledge to a greater and greater portion of the surrounding country. This topographical memory applies principally to prominent visual cues such as large optical patterns formed by hills, valleys, and villages. A bird released in unknown territory flies in an ever widening spiral until it discerns some familiar landmark; then it orients itself and flies home. Atmospheric conditions limiting visibility, as well as fog and snow, which change the appearance of the country, have a detrimental effect on the number of birds returning to the cote. Of 1,500 birds released at sea 500 kilometers west of Croisic, where no familiar landmarks were present, only 300 had returned in two days. The remainder were found scattered in England, Spain, Portugal, Algeria, Cape Verde, Egypt, and the Caucasus.⁽²⁸⁾

At present, the evidence does not justify the assumption of a specific directional sense. And since blind birds cannot return home from any distance whatever, homing behavior seems dependent on some form of visual stimulation.

TABLE IX
SUMMARY OF DATA OBTAINED BY THE DISCRIMINATION METHOD IN VARIOUS ANIMALS

ANIMAL	VISION					AUDITION		OLFACTION		GUSTATION	CUTANEOUS		Proprioceptive		Directional	
	Brightness	Size	Form	Color	Distance	Noise	Tone	Food Odors	Other Odors	*	Tactile	Thermal	*	*	N	N
Fish	*	*	?	*	*	P	P			*						
Turtles	*	*		*	*	P	P									
Guinea pigs	*	*		N		P	P									
Mice	*	*	N	N							*		*			
White rats	*	*	*	N	*	*	*		?	?		P				
Pigmented rats	*	*	*	N	*											
Rabbits	*	*	*	N	*	P										
Cats	*	*	*	N	*	P										
Porcupines	*	*	?	N	*											
Raccoons	*	*	?	N	*	P										
Dogs	*	*	*	N	*	P			*							
Chickens	*	*	?	*	*	P			*							
Monkeys	*	*	*	*	*	P							*			

Summary

Most of the data in Table IX have been obtained by the method of acquired differential response (fourth method, page 191). The blank spaces indicate no data; an "N", negative data; a question mark, some conflicting data; and an asterisk, positive experimental data. Spaces with a "P" (otherwise blank) indicate positive data in Chapters VI and VII, obtained by the first three methods listed on page 191. The number of unfilled spaces gives an idea of the possibilities for research in this field. Although these animals are known to have functioning sense organs of various kinds, they have not been systematically studied by the discrimination method.

EDITOR'S NOTE.—The reader should bear in mind that in Chapter VI, Professor Purdy dealt with sense organ function in general and presented data indicating that an animal is influenced by the stimulus. In this chapter Professor Fields deals with its more specialized aspects, such as the discrimination of relationships, qualities, and other abstractions; he presents in Table IX only data obtained by the method of acquired differential response, in which the animal is presented with an asymmetrical situation to which he must react (see page 109). This is the explanation of some of the apparent contradictions of the two chapters.

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CHAPTER VIII

The Neurology of Learning

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ALL learning involves, and in reality consists in, the modification of instinctive or reflex responses. Every stimulus originally gives rise to diffuse activity in the organism. In the process of learning, the actions resulting from a stimulus become more precise and limited. This does not mean that the learned action is simple: it may remain complex. But there may be differences in values for the individual parts of which the action was originally composed. Because of these differences in the amounts of the elements, the "learned reaction" may appear to be qualitatively different from the original reaction. Schematically this may be conceived as in the accompanying diagrams (Figure 29, A and B), in which only four different components of an activity are represented. In the diagrams, the sizes and lengths of the areas illustrate, respectively, the relative intensities and durations of the parts of the action. It will be noted that because of the different values of the parts, the second combination appears to be qualitatively different from the first; but such a diagrammatic difference is no greater than what is found in the course of the development of what is called a "learned" activity.

* This chapter was completed shortly before Dr. Franz's death on October 14, 1933.

The receiving organs and their nerves, the effector organs and their nerves, and the associative connectives in the central nervous system are the three necessary elements in learning. If a person has no eyes, or if he lacks the connections of the eyes with the brain, he cannot learn to

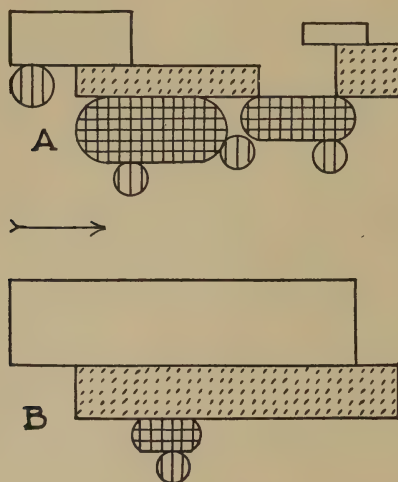


Fig. 29.—Illustrating how two actions, "A" and "B," resulting from the same stimulus, may be composed of the same kinds of fundamental elements in different quantities, the combinations giving rise to what appear to be quite dissimilar effects. *A* represents an unlearned, diffuse, disorganized action; *B* represents a learned or organized activity. The same four different elements are shown in both actions, but the quantities and the sequences differ.

react to visual stimuli. If both his arms are amputated, he is incapable of carrying out certain activities. If, thirdly, parts of his central nervous system have been destroyed, learning is not possible. However, if only one eye has been removed, some visual learning is possible. Also, if only one arm is amputated, some learning is also possible. In addition, recent investigation has demonstrated that if some parts of the central nervous system are re-

moved, learning is still possible. Much is known of the possibilities of learning, or of substituting activities, under conditions of receptor or effector limitations. We know less regarding the possibilities and the conditions of learning when parts of the central nervous system have been destroyed. The data we have help, however, towards an understanding of the neurological mechanisms required for the modification of the reflex or instinctive modes of action.

Although it is often assumed that the brain, and, more particularly, the cerebrum, is especially concerned in the processes of learning, it is known that modification of activities may be brought about through the mechanisms located in the spinal cord ⁽³⁾ and in the mid-brain. Moreover, such modifications seem to be relatively simple. Those modifications, or learnings, that involve school activities have attracted much attention psychologically, but they have not been amenable to much neurological investigation. Some of the fundamental processes have been investigated, especially those concerned with the learning of relatively simple acts by animals (for example, Watson's study of the rôle of kinæsthetic sensations in the rat in learning a maze). Subsequently it will be pointed out that in human learning the mechanisms are probably similar to, even though more complex than, those in the learning by rats or monkeys.

Although many observations of learning, both of humans who had parts of the brain destroyed by disease or by accident, and of animals experimentally deprived of parts of their brains, had previously been reported, systematic investigation of the problem has been confined to about the last thirty years. The exact cortical localization of complex mental functions was not acceptable to neurologists during the latter part of the last century, even though attention had been chiefly directed only to the correlation of motor, sensory, and speech functions with parts of the

cerebrum. The first attempt at a systematic investigation of the problem of learning in relation to the cerebrum seems to be that of the present writer, who reported ⁽¹²⁾ the results of experiments on the frontal lobes in relation to the production and retention of sensory-motor habits. That early work was carried on with cats, and extensions of similar investigations of the monkey brain were subsequently reported. ^(8, 11)

The method employed in these early investigations has been so extensively used in later work that it has become a recognized procedure for cerebral investigations, paralleling the stimulation method for the determination of motor functions that was used by Fritsch and Hitzig. ⁽²⁹⁾ The special procedure was a combination of the animal-learning investigation method, originally used by Lloyd Morgan and applied by Thorndike and many others, with the extirpation method used in the earlier experiments carried on by many physiologists and neurologists. Animals were trained to respond to definite situations and, after they had learned to react in a suitable manner, parts of their brains were removed so that it might be determined whether or not the learned reactions persisted. In addition, some animals were so tested that it might be learned whether or not, after the removal of certain brain areas, it was possible to bring about in them new habitual modes of reactions. This procedure, originally involving on the sensory side visual + kinaesthetic + tactile impressions, was subsequently claimed, but with slightly different sensory emphasis, by Kalischer ⁽²¹⁾ as his own original method for the determination of auditory and other functions of the cerebrum. With various modifications, the method of animal training plus extirpation has been used in many of the later investigations from the results of which our present concepts of cerebral-mental relations have developed.

Long before the publication of reports of the experiments on the frontal lobes to which reference has been made,

sporadic accounts were published regarding recoveries, or reëducation, of human subjects who were believed to have incurred destructions of parts of the central nervous system. Those accounts did not conform to the concept of definite functions for special parts of the nervous system. Because of this fact, they were disregarded in discussions of general neurological-mental relationships. Nevertheless, some of the possibilities of functional substitutions became well known, even though their relations to brain functions were not often considered.

One of the earliest of the attempts was the substitution treatment by Fraenkel in cases of *tabes dorsalis*. That disease brings about a degeneration of the nerve elements making up the dorsal columns of the spinal cord. Symptomatically, the patients lose their ability of accurate movement because of the loss of kinæsthetic sensory impulses. The kinæsthetic impulses seem, therefore, to be conveyed normally through those neuraxons that constitute the spinal dorsal columns. In some instances, patients seem to become incapable of movement; but the inability is a secondary phenomenon, due to the patients' attitude towards their disabilities. When the tabetic is given an extended course of special exercises, he becomes capable of walking and of carrying out other actions in an accurate manner. The substitution that was thought to take place in many of these cases, and that probably did take place, was that of a visual experience for a kinæsthetic one. The patient sometimes controlled his movements by watching them instead of having those normal feelings of movement coming from muscular changes and from the change in the positions of bones, and so forth, that consciously we usually disregard but that are obviously important for the performance of coördinated actions. It became known, however, that blind tabetics could recover an accuracy of movement through substitutions other than the visual ones. Regardless, therefore, of the kind of sensory substitution in these

patients, it is clear that a movement may be controlled by the use of afferent elements other than those that are normal. Because the reëducation is carried on through "conscious" control, it is believed that the substituted elements are related to activities of parts of the cerebrum. The conclusion is obvious: a person may learn to control an activity by the utilization of neurological elements not normally brought into play.

In addition to the reëducation possibilities associated with the sensory defects in *tabes dorsalis*, substitutions in more direct motor functions should be considered. A generation or more ago, the widely accepted view was that the motor functions of the cerebral cortex were well defined. Regardless of this concept of motor control, some orthopedic surgeons decided to try to improve cases of infantile paralysis by transplanting muscles or tendons from one part to an adjoining, but differently moving, part. Thus, a connection might be made between an unparalyzed muscle at the back of the leg and the front of the leg to replace a completely paralyzed muscle in the latter region. In some cases, this functional substitution was successful, and although a patient might not be able to manipulate the foot as well as he did prior to the paralysis, there was a functional return to a considerable degree. If we picture this state of affairs, schematically but very simply (as in Figure 30), we may see its bearing upon the general problem that concerns us.

When a muscle substitution of this kind is made, the recovery cannot be understood except as a change in the functional relationship of some cerebral elements as well as a change in the spatial relationship of the muscles. Even though the change appears to be primarily peripheral, the process of adjustment is essentially a cerebral replacement. It is a process of learning. Under the circumstances, a part of the brain that is not normally used, or not maximally used, for a special series of actions must be

utilized for carrying out the changed activities. In relation to the diagrams shown in Figure 30, we may set forth the altered state of affairs as follows. Diagram A: Cerebral areas (or, less likely, special individual cells) *a* and *b* control, respectively, the actions of muscles (or muscle groups) *a'* and *b'* through cells in the spinal cord (*SC*).

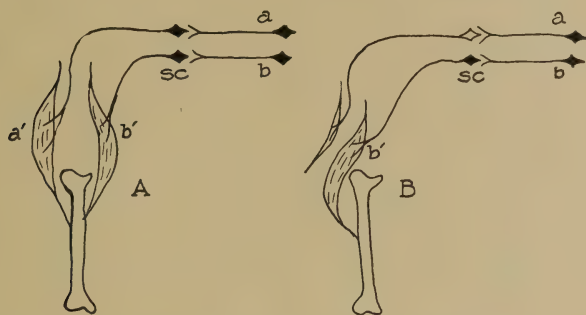


Fig. 30.—Representing the change of cerebral relations in cases of infantile paralysis in which muscle or tendon transplantation has been carried out. *A*, normal relations; *B*, after paralysis and surgical procedure. *a'* and *b'* are muscles represented, respectively, by cerebral areas *a* and *b*, which act through spinal-cord cells (*SC*). Paralysis of muscle *a'*, resulting from destruction of spinal-cord cells (in *B*), is compensated for by the use of muscle *b'*. In such cases, cerebral area *b* after the operation controls an action different from that which it controls in the normal state.

When (Diagram B), because of destruction of some of the spinal cord cells, muscle *a'* degenerates and is surgically replaced with muscle *b'*, the action formerly performed by the cerebral cells and the muscle (*a-a'*) is carried out by the combination *b-b'*.

In the conditions of *tabes dorsalis* and of infantile paralysis, therefore, we have evidence of the possibility of changing various functions of the cerebrum. Although the conditions in these two states are pathological, the replacement in both cases is nevertheless illustrative of the possi-

bilities of normal learning. It is, in fact, learning—the modification of original tendencies.

Many other facts collected from patients with lesions of parts of the nervous system and from animal experimentation also help towards a better appreciation of the cerebral conditions in learning. The experiments with animals are not only suggestive, but they have great value both because the brains of animals are much less complex than the human brain, and because destructions may be limited to those parts that the investigator wishes to study.

The early experiments on the cat, by the writer,⁽¹²⁾ pointed to the frontal lobes as links in the neurological chain important for learning, although some other cerebral areas did not appear to be involved in habit formation. Subsequent experiments on monkeys^(8, 11) pointed in the same direction. Similar experiments by Kalischer⁽³⁴⁾ and by Swift⁽⁴⁸⁾ and, much later, the work of Cameron⁽⁴⁾ support the general conclusions, although corresponding experiments of Jacobsen⁽³³⁾ have given negative results. Lashley and the writer⁽⁴⁰⁾ found that in rats the removal of parts of the simple brains tended to interfere with the learned reactions, but that in many instances large areas of the cerebral cortex could be destroyed without affecting the ability of the animals to react in a normal manner. A considerable number of investigations by Lashley, summed up by him at later dates,^(36, 37, 38) also point to the inadequacy of the conception of a special part of the brain as a so-called "center" for intellectual states or for the acquisition and retention of habits. Lashley's results are of great importance for an understanding of the neurological conditions in learning. Although the results have been interpreted to mean that all parts of the cerebrum are equally valuable for sensory, motor, and associational processes, that interpretation has been adversely criticized (for example, by Hunter⁽³²⁾). It should also be noted that for some of the cerebral sensory functions, Lashley⁽³⁵⁾ has con-

tended that the cerebral cortical areas are not "equi-potential."

Lashley⁽³⁷⁾ has been able to show that learning is possible for a rat that has had a large part of the cerebral cortex destroyed. The accompanying curves (Figure 31)

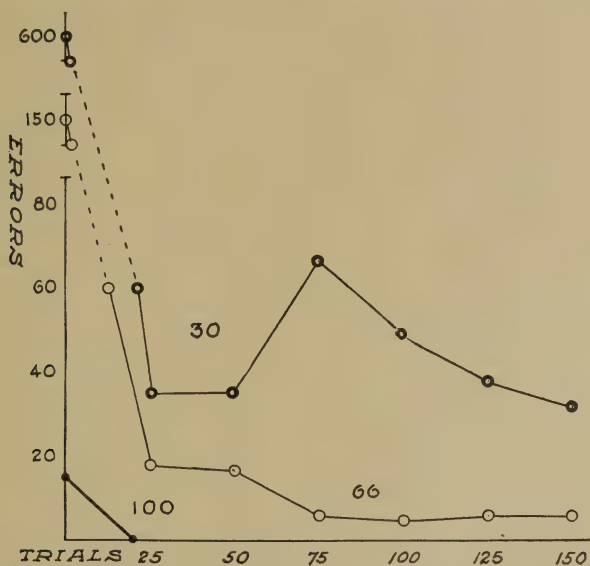


Fig. 31.—Illustrating the speed and completeness of learning of rats in a maze, in accordance with amounts of cerebral cortex they possessed. Normal animals were 100 per cent; two other groups of animals had, respectively, only about two-thirds and one-third of the normal amount of cortex. The normal animals made very few mistakes and took only a short time for learning; those with two-thirds of the cortex took much longer, and the learning was less complete after many more trials; and those with only one-third of the cortex showed the slowest and least complete learning. (After Lashley, modified.)

show the general results that he has reported. He has found that after about one-third of the cerebrum has been removed, learning is possible but is much slower than it is for an animal with a cerebrum intact, and is not so com-

plete. When two-thirds of the cerebrum is removed, learning is still possible; but it is slower and less complete still than it is for the animal that retains two-thirds of the cerebrum. Results of this kind may be interpreted in several ways. The interpretation that pertains to the present discussion is that the mechanisms for learning are not fixed, in the sense of being single and separate, but are variable, in the sense of there being many ways in which learning is brought about. When an animal has the usual quantity of cerebral matter, learning is relatively easy, because the connecting pathways for the sensory-motor impulses are freely usable. When parts of the cerebrum have been removed, some of the more readily usable pathways may be obliterated. Under these conditions, other, less readily used pathways have to be employed for bringing about an association of the sensory experiences and the reacting organs. When, therefore, large parts of the cerebrum are removed, circuitous or seldom used mechanisms may need to be set in action. Closely allied to the results obtained by Lashley are those that have been reported by Gemelli and Pastori,⁽³⁰⁾ who experimented with chickens and pigeons. These authors found that only a small part of the cerebrum was needed by those birds in learning to discriminate colors and in relearning.

Numerous other experimental results with animals, including some that do not appear to bear directly upon the problem of learning, point in the same direction. Regarding the motor functions, the writer,⁽²²⁾ Stout,⁽⁴⁷⁾ Leyton and Sherrington,⁽⁴¹⁾ and others have shown that the same action does not always follow the application of the same electrical stimulus to the same point of the cerebral cortex. These results have been interpreted to mean that certain time and intensity relationships (chronaxies) of the cortical mechanisms are important elements in carrying out cerebral-motor actions. They also indicate the probable importance of the

recurrence of similar conditions in the formation of associations of a sensory-motor character.

The phenomena of the conditioned reflexes* have often been referred to as the fundamentals for all learning.⁽⁴⁴⁾ The conditioned reflex may be considered to be the paradigm for an understanding of changing modes of reactions; but except for the simplest physiological activities, it is an unsatisfactory interpretation, and the concept must be greatly stretched to explain even the simplest forms of learning by man. The experimental pattern for the formation of a conditioned reflex is relatively uncomplicated and may be described in the following manner: There are presented simultaneously two stimuli, of different characters, to one of which the animal normally gives an obvious reaction. Thus, if a bell is rung at the same time that food is shown to a hungry dog, the animal's salivary glands secrete because food is exhibited. If, now, the combination of the auditory and food stimuli is repeated frequently, the time arrives when the sound of the bell by itself produces a salivary flow. This result is called a "conditioned reflex."

The production of any conditioned reflex is dependent upon the presence in the nervous system of pathways that do not normally function to a maximum degree (see Figure 32), but that may become of great importance because of the frequent receipt of the same kind of stimulus. At present, our view of neurone connections is that any one neurone, at or shortly after birth, has developed its axons and collaterals to the point where all of the anatomical connections through which it may subsequently become functionally capable of reacting are present. If, for example, a visual stimulus is presented, the connections are available (*a*) for blushing in the face, (*b*) for changes in heart rhythm, (*c*) for movements of the stomach and in-

* See Chapters IX and XII for a more detailed outline and critique of this subject.

testines, (*d*) for secretory changes in the skin and other organs, (*e*) for motor adjustments of the head, of the trunk, of the legs, and of the arms, as well as (*f*) for changes in

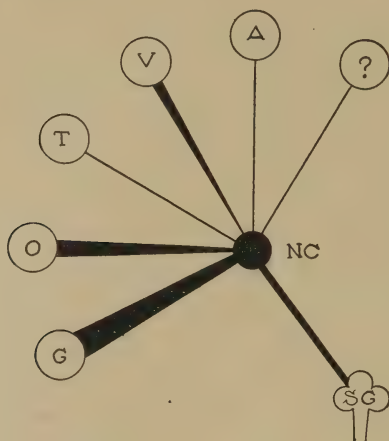


Fig. 32.—Illustrating different sense stimuli that may give rise to a reaction, with special reference to the conditioned reflex. *G*, *O*, *T*, *V*, *A*, and *?* may represent, respectively: the gustatory, olfactory, tactile, visual, auditory, and other kinds of stimuli. *SG* is the salivary gland, which receives impulses from the sense organs through its nerve center *NC*. The different widths of the connecting elements from the sense organs represent schematically the greater or less potency of “original” effects, the relative values of which may be changed through training. A similar diagram, with muscles pictured in place of a gland, and with different connecting values, may represent any other kind of reaction. Compare Fig. 33, in which changes in the reacting mechanism are schematized.

the pupil and in the position of the eyes. Some of the pathways are more usable—more patent and more direct—than are others. This means that following certain stimuli, reactions are more apparent and stronger in some reacting structures than in others. These facts may be understood if reference is made to Figure 32.

To consider a concrete example may help to make obvious the possibilities of reaction differences even beyond

those of the conditioned-reflex level (see Figure 33). Suppose that I have a colored picture of a common fruit—say, an apple—to which I am to respond with a word when the picture is shown. The picture is the stimulus, *S*. My re-

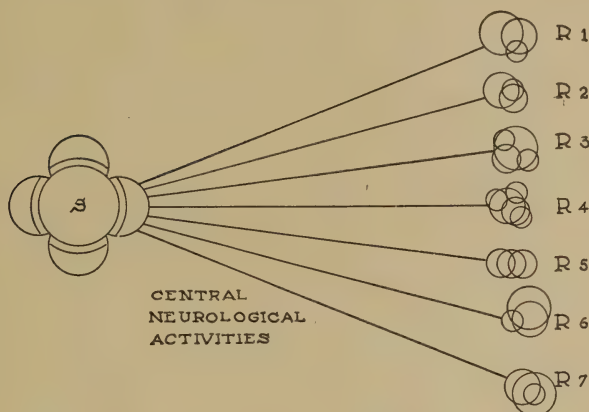


Fig. 33.—Showing how a sensory stimulus (“*S*”) may give rise to many reactions of different characters (“*R1*” to “*R7*”). The reactions may be similar in components (see also Fig. 29). One combination, however, may become developed as the “normal” reaction—for example, *R6*; but by later training it may be replaced with another, as *R1*. Compare with Fig. 32, in which is illustrated the production of similar effects from different sensory stimuli.

action may be any one of a number of possibilities: *R1*, saying, “Apple”; *R2*, vocally spelling out the word; *R3*, writing the word by hand; *R4*, writing the word on a typewriter; *R5*, vocalizing the word in German; *R6*, vocalizing the word in French; *R7*, vocalizing the word in Italian. Other reactions are also possible. Let us assume that *R1* is the most readily produced reaction under what are called “normal” conditions. If the conditions are changed—suppose that I am in a restaurant with waiters and patrons speaking French: even though I have not learned to speak that language fluently, the stimulus of the picture may

give rise to *R6* without much difficulty; for the moment, *R1* is replaced with *R6*. If the circumstances are changed after a longer period of time—for example, after several months' sojourn in the west of France—the ease of *R6* may be as great as that of *R1*. Many replacements other than those of a speech character are also possible.⁽²²⁾

In the conditioned reflex, we find the possibility of the substitution of one kind of stimulus for a more common stimulus in the bringing about of a reaction. On the other hand, we find that a certain well-defined stimulus may give rise to different kinds of reactions at different times. It is these two types of adjustments that are basic in all learning. The two types are complementary, and they frequently work together.

From the standpoint of the neurological connections, however, it must not be assumed that the sensory stimuli go to cerebral areas that are independent in their actions. Ample evidence is at hand to show that any sense stimulus has an effect that is widespread. Much of this evidence has been due to recent investigations. Lashley has been able to show that rats may learn to react to visual stimuli even when the so-called visual areas are destroyed. If parts of the visual area are destroyed, habits may still be organized in relation to visual intensities; but it is known that the exactness decreases, and the time of learning increases, in accordance with the amounts of the destroyed areas. Other experiments have shown that in animals' brains, visual and other stimulations bring about electrical changes in areas that are widespread. These facts indicate that stimuli may have effects over large parts of the cerebrum; but the experiments also show what appear to be foci, where the changes are great, with decreasing effects for the surrounding regions. These results, reported by Perkins⁽⁴⁵⁾ and by Bartley,⁽¹⁾ need not be directly interpreted to mean that at the points of greatest change there is more intense (sensory) function; but they may mean

that sensory functions are due to or are dependent upon massive or widespread cerebral action.

Additional important information regarding the relation of the cerebrum to learning has been gained from a series of observations in the fields of touch and vision.* The experiments show that in learning there is a widespread effect in the cerebrum. If, for example, an area on the right thigh is repeatedly stimulated by a number of geometric forms applied to the skin, the subject learns to discriminate among them after a considerable amount of practice. If, following the learning with that part of the skin, the opposite thigh is tested, it is found that discrimination again takes place. The training, therefore, is not limited to the circumscribed skin area, nor to a localized cerebral area with which the skin area is supposedly connected. The area of educated skin is limited, to be sure, but the special training results in a generalized ability. Because of this, we may conclude that the diffusion effect is likely to be cerebral in character. An extension of the experimental procedure has shown that the diffusion effect is not only correspondingly contralateral, but also excentrically homolateral; that is, tests of the opposite side of the body show an ability of discrimination, and so, to almost an equal degree, do some of the far-off areas on the same side of the body.

In the field of vision, similar results have been discovered. If one area of the retina (and its cerebral connections) has been trained, adjoining retinal areas (with their cerebral connections) show the effects of the training. It was also found that if only one eye was used in the training series, there was a "transfer" to the other eye. Furthermore, it was discovered that if two stimuli are shown in such a way that one of them is "seen" with the right hemisphere and the other with the left hemisphere, the two may be

* See references 15, 16, 23, 24, 26, and 27 in the bibliography.

simultaneously apprehended—when a combination of the two takes place. If the stimulus for the right cerebral hemisphere is of such a character that it may be combined in meaning with that for the left hemisphere, combination of meaning also results. To make the latter statement concrete: it has been found that if the two letters H E are exposed so that they are “taken in” with the right half of one retina and the right side of the cerebrum, and A D with the left half of the retina and the left side of the cerebrum, the four letters are apprehended together, that is, combined into the one word HEAD, and they are understood. This means that in such a process the unification is probably brought about by cerebral connections between the two hemispheres.

In addition, evidence has been accumulated respecting the relative values of the two cerebral hemispheres in learning. It has frequently been said that right-handedness is due to a functional dominance of the left hemisphere, and that this cerebral dominance is important for the acquisition of special skills and other accomplishments. This assertion seems to be supported by evidences from neuropathological states, especially those present during losses of speech (aphasias) associated with cerebral destructions. The aphasias are said to be due mainly, if not exclusively, to destructions, in right-handed persons, in the left half of the brain. If this distinctive left cerebral dominance were actually present in right-handed persons, and if there were a corresponding right cerebral dominance in the left-handed, it should follow that each of the two halves of the brain would function well, for learning, to a degree in accordance with the handedness and the supposed dominance. This tentative conclusion was not verified by the facts. Some of the left-handed showed a greater learning ability for nonsense forms visually apprehended with the left cerebral hemisphere, and some of the right-handed learned corresponding visual problems better with the right

cerebral hemisphere. In the experiments on "reading" mentioned in the preceding paragraph, it was found that the right-handed subjects learned to read more readily those letters that were the stimuli for the right hemisphere than those that were the stimuli for the left hemisphere. The learning with one or with the other cerebral hemisphere appears, therefore, to be dependent upon factors other than handedness. And handedness is due to factors partly outside of hemispherical dominance.

It may be that "attention" to an expected stimulus from a given direction is an important element in the apprehension of visual forms or words with the left or with the right hemisphere, respectively. However, we know nothing of the possibilities of producing unilateral cerebral functioning in connection with attentive states. If "attention" is conceived to be an important factor in the determination of the use of a cerebral hemisphere, it follows that a unilateral superiority is very slight or that the dominance may be shifted without difficulty. In either case, it cannot have the commanding value that has been imputed to it. Certainly for the performance by a person of an act following a visual impression, it is important that the reception of the stimulus by either side of the cerebrum be followed by appropriate muscular reactions involving the right or the left half, or both halves, of the body. For the learning of visual-motor reactions, there is ample evidence to warrant the belief that one cerebral hemisphere is not more important than the other. Other evidence, that in relation to the speech functions, does appear to point to the conclusion of a cerebral dominance. This evidence we shall now consider.

About seventy years ago, Broca reported the case of a patient who lost the ability of vocal speech because of a destruction of the cerebral cortex in the lower portion of the frontal convolution of the left hemisphere. This report was followed by many others that tended to support

the view that in right-handed persons the functions of speech are mediated through activities of the left cerebral cortex. Although many negative cases have been cited and discussed by Von Monakow and others, the general conclusion has been widely accepted. The reported "facts" seemed at first to show a distinct cerebral localization for the elements of speech, and the relations of these elements to activities of cerebral areas were reported in exact terms. Nevertheless, many patients showed defects that could not be brought into one picture, except as relatively unrelated pieces. Efforts to unite the different pieces into definite patterns were made, but they were unsatisfactory—partly because the aphasic at times reacquired some of his former ability. If the destroyed areas are speech areas, how can a patient reacquire speech? Are there accessory speech areas or mechanisms? To obviate an extended discussion here, we may tentatively admit that the cerebral defects that often give rise to the disabilities of speech in right-handed persons are those in the left cerebral hemisphere. As a corollary of this, there has also been deduced the conclusion that in the left cerebral hemisphere the associative speech mechanisms are to be found. The final acceptance of the main conclusion and its corollary is, however, not to be determined solely on the clinico-pathological findings that have been mentioned above. We may be willing to subscribe to the view that the mechanisms of speech are interfered with when the left cerebral hemisphere is partly destroyed, but we are not compelled thereby to conclude that the mechanisms of speech consist exclusively in the neurones of that hemisphere.

Some of the clearest conditions in learning in which activity of the cerebrum is believed to be the main factor are illustrated by the reacquisition of speech reactions by the aphasic. The aphasic, as Head ⁽³¹⁾ has expressed it, has lost some of his capacity for symbolic thinking and expression. This fact may be evidenced on the expressive

side by the aphasic's inability to name objects, or to use words in their proper connection, or to combine the words into suitable clause or sentence structures, or to express the meanings of complex situations. Similar defects are found in relation to the understanding of speech symbols. These more recent concepts of speech function are in contrast to the older views, which conceived the aphasias primarily to be losses of images—visual, auditory, kinæsthetic, and so on. It is a fact that the aphasic does not necessarily lose his "ideas," as numerous accounts by patients testify. The aphasic shows a loss of ability to associate the reaction with the sensory or perceptual situation he experiences. He may see a picture and be able to show by pantomime or by writing what it involves, but he may not be able to formulate the verbal response. Conversely, he may be able to use many words, but he may not be able to give forth the special word he should vocalize. Thus, an aphasic who was asked to tell what a colored picture of a box of strawberries was replied somewhat as follows: "I know, but I can't say it. My wife bought some yesterday. She's making strawberry jam. Oh! Strawberries." Another aphasic described the accident that caused his defect as follows: "I had to go early, and I got the things, and went on, but stopped for a penny, and then I got going and down the place there came the thing and that's all." His account can be understood by comparing it with the following: He left home early to get some material needed in the work on which he was engaged; having obtained the materials, which he took in his car, he drove toward the place where he was working; on the way, he stopped to buy a penny newspaper, and after obtaining it he drove on; but when he was crossing a street, another automobile came at a rapid rate down a hill and struck his car, and that was the last he knew. Many aphasics appear to be limited to the expressions "yes" and "no," but at least in some instances it is certain that these words are the "easy" re-

sponses and not the "only" responses that they can make.⁽²⁰⁾ The aphasic, moreover, often recognizes his defect and is inhibited because of it. Somewhat similar statements may be made regarding other speech manifestations.

Even though the aphasic has lost some of his ability to understand or to express himself, it is possible for him to recover or to be reëducated to the point where he does understand and does express himself.^(14, 19) In experiments on relearning,⁽¹⁴⁾ it was found that the curve of acquisition is much like the learning curve for a normal person, but is prolonged in time. If, as in the cases that have been reported, there have been extensive cerebral destructions comparable with the speech losses (to the extent of the retention of only "yes" and "no"), the reëducation process must include areas that are not usually thought to be concerned with the production of speech. Here, then, is an example of learning with a part of the brain that is not thought to be used normally for that purpose.

The phenomena of speech reacquisition help towards an understanding of other relearnings after destructions have brought about losses of function. It is now generally recognized that after the occurrence of a cerebral paralysis in man and in animals, the defect need not be permanent.^(28, 42, 46) Recovery of motor control can be brought about, although it may not be possible for a patient to attain the accuracy and the speed of his normal accomplishment. It is also known⁽²⁾ that, after destruction of the postcentral cerebral cortex, which results in a loss of tactile discrimination and localization, the area of the skin that has been involved may be retrained (with the use of other parts of the brain) to discriminate and localize. The important fact is that when speech, movement, or a form of perception has been apparently lost because of a brain destruction, the loss does not mean a complete inability for the future: there is a possibility of learning, perhaps through the use of other brain parts.

In connection with relearning by the aphasic, it is important to note that after a patient has relearned to use some words, there are great fluctuations from day to day and sometimes even from hour to hour.⁽⁹⁾ Both the motor and the sensory relearnings are also affected, for better or for worse, by the situations in which the patient finds himself. These variations in ability indicate that the mechanisms are not fixed. They show that the situation (or Gestalt) makes for ease or difficulty of action, including vocalization, and they also show that the cerebral mechanisms are influenced by apparently slight variations in stimuli, or by attitude. The aphasic may be able to give the names of objects swiftly and accurately to his instructor, but the presence of an unfamiliar observer in the room may make him revert to an almost inarticulate state. From this fact it can be seen that a stimulus, let us say a visual one such as a ball, does not result in a simple chain of neurone activities. It does not give rise to a nerve impulse that proceeds to a sensory point on the cerebral cortex, from which an effect passes to the cerebral motor areas to produce coördinate movements of lips, tongue, and other parts needed for vocalization. Nor does any other stimulus, whether simple or complex, bring about responses in such a simple fashion. It is becoming more apparent that there are many factors working at one time, together or in opposition, and that the ability to carry out a learned reaction is dependent upon the simultaneous and successive working of many parts of the cerebrum. This is what the writer has set forth in previous discussions of cerebral function,* but the statement must not be interpreted to mean that every part of the cerebrum is used for every act of speech or for the understanding of every word a person hears or reads. Many parts of the cerebrum may be used for a

* See references 5, 6, 7, 10, and 18 in the bibliography.

mental process, but it does not seem likely that every part is used for every one.

For an understanding of the neurological processes in learning, one must have some general conception of how the brain works. Such a conception may be inadequate to account for all of the old facts, and it may not be inclusive for those that will be discovered. Nevertheless, a general hypothesis has value, because not only may it present a tentative explanation, but it leads to future investigation and reinterpretation. Lashley's equipotential view⁽³⁷⁾ may need modification, as has been admitted by him,⁽³⁵⁾ and so may the views of the present writer; however, analogies are useful to help picture what is going on.

The nervous system is to be looked at as a series of connections or pathways that are complex and that may bring about relations between two parts of the body (the sense organs and the reacting organs) in a variety of ways. It may also be likened to a city, where one may approach a given corner by many routes, some direct and others more circuitous. One may go to a grocery store by several routes and achieve the same result: buying a loaf of bread, provided one has the money. On the other hand, it may "normally" be possible to walk one block west and two blocks south to make the purchase; but if that store has been destroyed by fire, one may obtain a similar result, although with a greater expenditure of energy, by going four blocks west and three blocks north, or by going six blocks south and two blocks east. We may also get the same bodily reaction through diverse sense experiences. Thus, the verbalization "ball" may result from the sight of a golf ball, a tennis ball, a baseball, or a football. (See again Figures 32 and 33.) To carry the analogy further, we may say that it is not only the need of a loaf of bread that starts us to a grocery, but many other needs that are not related to hunger. We may go to purchase a broom or a bar of soap. The same series of general reactions

may be produced by different needs or stimuli. There are, however, certain limitations to the number of reactions. One does not go to a grocery to purchase a suit of clothes, books, or a piano. So also there may be a number of possibilities of reëducation effects, but these effects may be limited, as the work of Lashley and others indicates.

We may also liken cerebral conditions with geographical relations in a country or a state. We may go from one place to another by airplane, by automobile, by boat, or by railroad, or we may walk. The pathways may differ, but the starting and the finishing points are the same. The selection of a conveyance may depend upon many factors—storms that have been reported, the availability of an airplane field, and so forth. At the same time, it may be that we can travel to some places only by a combination of railroad and walking, and to other places by a combination of airplane and automobile. In addition, we may reach a given point from any other given point in the State. These analogies may be applied to the central nervous connections, although not too specifically. The pathways between the receptor and the effector organs may be fixed anatomically, but there may be many functional paths. The number of anatomical and functional paths may also be fixed, and there may not be more than ten, or perhaps not more than two, from which to select. The selection of the path taken at one time may not be determinable by the person but may be due to many factors, both general and special. The same functional path may not always be used under what appear to be similar conditions. It may also be that there are no fixed functional paths.

Diversity of action from time to time and diffusion of action, which characterize the unlearned reaction, are the correlates of the "normal" use of the many neurological pathways. And, owing to this, learning comes about because of a relative fixity of special paths. Difficulties in

the organization of special habit systems, and corresponding difficulties in the replacement of habitual modes of reaction, point, respectively, to the functional diversities and to relative functional fixities. These, therefore, are some of the more important neurological correlates of learning: (a) the numerous available pathways from sense organ to muscle, which permit a variety of adaptations; (b) the possibilities of stabilization of a functional pathway so that the reaction becomes habitual. Much has been learned about the diversity of the connections. Less is known about the conditions in stabilization. Both, however, are necessary neurological bases that make learning possible. In animals with relatively simple nervous systems, the diversity is slight and the learning that takes place is of relatively simple things. The great masses of nerve structures in man permit great variability in reaction, and they make possible a multitude of specialized sensory-motor combinations and a mass of ideational associations. Perhaps it should also be said that, regardless of the psychological terms by which they may be described, sensory-motor habits and habits of thought are the ends of learning.

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CHAPTER IX

The Conditioned Reflex

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IN a volume concerned with the field of comparative psychology, the conditioned reflex merits separate discussion for the following reason. It has become a leading concept of behavioristic doctrine and has been used to explain many of the most intricate phenomena of animal and human behavior. As such behavioristic explanations multiply, actual experimental investigation does not increase correspondingly. Perhaps the too ready acceptance or rejection of Pavlov's theory of behavior has discouraged the less pretentious labors of experimentation. The working concepts of a scientific theory may fairly be regarded as part of the investigator's laboratory equipment. In this sense, each concept is constructed in the laboratory and is a tool to be used, as the kymograph and drop-recorder are used by the physiologist, to aid his observation and thinking. Many concepts and working hypotheses should never be taken from the laboratory to the study. When they are so transferred, their usefulness for effective thinking often vanishes because their humble origin in the practical details of laboratory procedure is forgotten.

Since the publication of I. P. Pavlov's two volumes of lectures concerning animal and human conduct,^(10, 11) it is unnecessary to attempt a comprehensive review of the monumental structure of experimental detail upon which

his theory of conditioned reflex action is based. It is essential, however, to attempt to visualize the actual experimental setting in which the conditioned salivary reflexes of the dog have been investigated, because each term—such as *irradiation*, *induction*, and *extinction*—employed by Pavlov in expounding his theory of the conditioned reflex has derived its meaning from the context of some particular group of experiments concerned with salivary secretion in the dog. Hence, this brief chapter will center upon a critical discussion of the *conditioned reflex method*. We shall first of all describe the procedure followed by Pavlov in establishing salivary conditioned reflexes in the dog, and then proceed to review the modifications of the technique necessary for the study of the behavior of other animals. This discussion of the method will naturally suggest comments upon the theory, but a comprehensive and critical analysis of the theory of the conditioned reflex will not be attempted in this chapter. (But see Chapter XII.) It is hoped that what follows will stimulate the reader to attempt this fascinating exercise in the logic of science.

Pavlov's Work on Salivary Reflexes

In order to establish conditioned salivary reflexes in the dog according to Pavlov's procedure, the papilla of the parotid duct must be transferred to the cheek. This simple surgical procedure is fully described by Podkopaew.⁽¹³⁾ When the dog salivates, a portion of the secretion is now diverted to the surface of the cheek. If a hollow vessel* is hermetically sealed over the papilla of the duct, and if this vessel is connected to a horizontal glass manometer tube filled with colored liquid, which may be placed in an adjoining room, secretion from the duct will displace the air in the vessel and cause the colored fluid to move along

* A common mistake is made by psychologists in the statement that a cannula is inserted into the duct.

the manometer tube, which is calibrated in 1/100 cubic-centimeter divisions. By this simple means, it is possible to measure at a distance the rate and quantity of saliva secreted by the dog under a wide range of experimental conditions. The experimenter, viewing the animal through a periscope, may continuously observe its behavior and at the same time estimate from the manometer the rate and quantity of salivary secretion evoked by a given situation. If the displaced fluid is an electrolyte, it may actuate an electrolytic drop-recorder, and a graph of the secretion may be obtained on a moving strip of paper.

The dog in which conditioned reflexes are to be established is taught to remain alone on a table in a soundproof chamber, where he is accustomed to receive food. A rotating platform bearing a number of small food dishes is enclosed in a box with an opening that exposes one of these dishes at a time. The dog consumes the food in each dish as it appears beneath the opening and learns to watch for the appearance of a new dish of food. The empty food dish claims his complete attention, so that no harness is necessary to keep him on the table until the following portion of food is presented by the rotation of the platform.

Figures 34 and 35 illustrate the arrangements just described. Typical records are shown in Figure 36.* The essential features of the method are, first, the isolation of the animal in a room where every external influence acting on its receptors is under experimental control and where equal quantities of food may be mechanically presented to the dog; second, the removal to another room of the chief source of uncontrolled stimuli—the observer himself. Under these circumstances, a conditioned reflex is established as follows. If a pure tone generated by an audio-oscillator

*These figures depict the conditioned reflex laboratory in the Department of Physiology, McGill University, with sample tracings from the recording system shown in Figure 35. (Used with the kind permission of Professor John Tait.)



Fig. 34

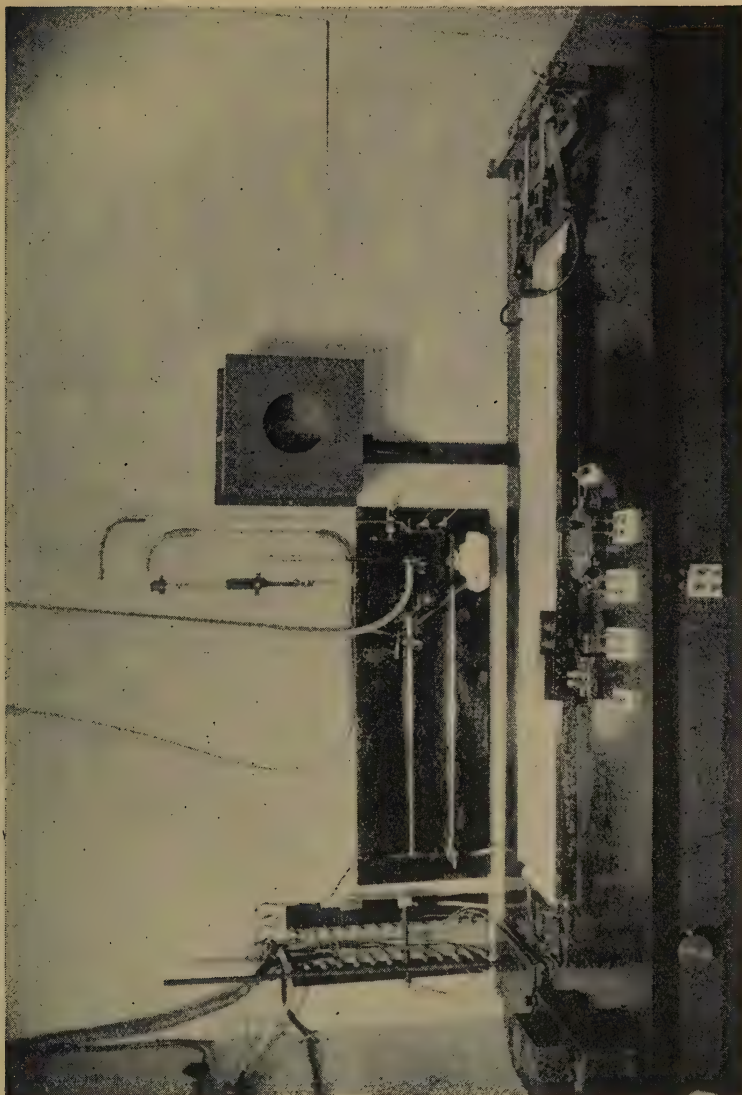


Fig. 35

is presented to the dog for five seconds by means of a loud-speaker placed in front of him, and then food (moistened meat powder and bread crumbs) is supplied by the device mentioned above, after a variable number (from 5 to 50)

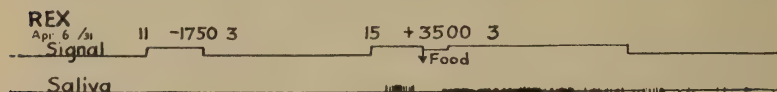


Fig. 36

of presentations of the tone, each of which is followed by food, the tone will become a signal for food and will evoke the secretion of saliva. The tone, which previously had no effect upon the salivary gland, has now acquired the same property of stimulating the reflex secretion of saliva as the presence of food in the dog's mouth. The tone has become a *conditioned stimulus*, and its action arouses an auditory conditioned salivary reflex. When the food is taken into the mouth,* the salivary secretion is due to an *unconditioned reflex*. From day to day, the duration of the tone is increased, and if the saliva still begins to flow within a few seconds (between 2 and 5) of the beginning of the tone, its duration may be extended to 30 seconds or even to a minute. When the conditioned reflex reaches this stage of development, quantitative study is possible, the quantity of saliva in .01 cubic-centimeter units secreted during the 30 seconds' action of the tone expressing the magnitude of the auditory conditioned reflex. The newly formed conditioned reflex is easily weakened or suppressed. If, before or shortly after the tone begins, a sudden change in the environment occurs, the secretion of saliva will be diminished or may be absent. This is called by Pavlov

*It seems strange that psychologists almost without exception refer to the secretion of saliva when the dog sees and smells food as an unconditioned reflex. This is wrong. The unconditioned reflex is evoked by the stimulation of the receptors in the buccal cavity during the eating of the food.

external inhibition and is due, according to him, to the fact that the change in the environment arouses another unconditioned reaction, the investigatory reflex, which is stronger than the conditioned reflex and inhibits it just as the scratch reflex in the spinal dog* is inhibited by the biologically more important flexion reflex to nocuous stimulation of the limb. Unlike the flexion reflex, however, the investigatory reflex rapidly disappears when the same change in the environment occurs a number of times. The new stimulus loses its novelty and can no longer yield the response appropriate to unfamiliar stimuli. It is to guard against the arousal of the investigatory reaction that the dog is confined to the quiet, rigidly controlled environment provided by a soundproof room with artificial illumination.

The new reflex exhibits another fundamental property. If the conditioned stimulus is a tone of 435 cycles, other tones, such as those of 100 or 1,000 cycles, will also arouse secretion when presented for the first time. The conditioned reflex in its early stages is, therefore, generalized. As training is continued, the reflex becomes more specific, so that tones more and more closely resembling the training tone (conditioned stimulus) will fail to produce a secretory response at the first application.

The specificity of the new conditioned reflex may be more easily and quickly attained by another procedure. After thirty or forty repetitions of the application of the tone of 435 cycles followed by food, a tone of 1,000 cycles is given as a stimulus but with no food following it. At first, because of the generalization of the auditory conditioned reflex, 1,000 cycles may evoke as much secretion during thirty seconds as the training stimulus, 435 cycles. With repetition, however, the secretory response to 1,000

* A dog in which the higher portion of the nervous system is cut away, causing the animal's environment to shrink until it is coextensive with body surface.

cycles gradually diminishes, and if food never follows this tone, its effect on the salivary gland is finally abolished for the time being. This phenomenon Pavlov calls *extinction*. If, during a single experiment, the conditioned reflex to tone 1,000 is extinguished, it will be found that on the next day, the salivary response to this sound will reappear. It can now be extinguished more rapidly, but, after a rest, is again restored. It is now still more easily extinguished. Finally, the tone of 1,000 cycles regularly fails to evoke salivary secretion. The stimulus is not, however, without action on the dog's nervous system. If tone 1,000 is presented for 30 seconds (no food being given), and then after a minute the training tone 435 is sounded for 30 seconds, little or no secretion may be observed. The tone that has been associated with *no food* has become inhibitory in action, and its effect, lingering on in the central nervous system, quells the excitation aroused by the signal for food (tone 435). This phenomenon is referred to as *successive inhibition*. Reasoning thus from the experimental data, Pavlov classifies conditioned reflexes as positive, or excitatory, and negative, or inhibitory—following the conventional classification of spinal reflexes. The extinguished positive conditioned reflex becomes a negative conditioned reflex, central excitation being replaced with inhibition.

The tone of 1,000 cycles, after it has become a negative conditioned stimulus, can be used to demonstrate another fundamental behavior phenomenon. If the negative conditioned stimulus (tone 1,000) is presented for 30 seconds, and then a pause of only from 15 to 30 seconds ensues before the positive conditioned stimulus, tone 435, is sounded, it will be observed that this positive tone now induces a flow of saliva from 50 per cent to 100 per cent greater than is commonly obtained during its 30 seconds of action. The marked increase in the magnitude of the positive conditioned reflex when it almost immediately follows a negative

conditioned reflex is named *positive induction* by Pavlov and is likened to the phenomenon of contrast in retinal stimulation. The converse phenomenon of *negative induction* is also described by him. According to his theory, a focus of excitation in the cerebral cortex induces at its periphery a state of inhibition (negative induction), whereas a corresponding area of inhibition induces at its periphery a state of excitation (positive induction).

If the stimulus for a newly established negative conditioned reflex (that is to say, a newly extinguished positive reflex) is presented during or just following a sudden change in the environment, the orienting reaction will be initiated, and this will suppress or inhibit the newly formed inhibitory conditioned reflex, and, as a consequence, the positive reflex from which it was transformed will be disclosed. For example, if a sudden noise or bright light acts on the dog's receptors just as the tone of 1,000 cycles is presented, this tone will now evoke the secretion of saliva. This is the phenomenon of external inhibition as it applies to the negative conditioned reflex. It is referred to in Pavlov's writings as *disinhibition*. It is, according to his theory, an instance of the inhibition of inhibition.

It is possible to retard the onset of salivation when the signal for food is given. If the conditioned reflex to a tone of 435 cycles is regularly elicited by the presentation of the tone for 30 seconds, the latent period from the beginning of the sound until saliva appears will be of relatively short duration (from 2 to 5 seconds), as mentioned above. Once again the duration of the conditioned stimulus is gradually increased, over a period of several days, to one minute, to two minutes, and finally to three minutes. The latent period will gradually lengthen also, until it becomes as long as two minutes when the tone continues for three minutes before the food is given. Such a response with a long latent period is a delayed or retarded conditioned reflex. Pavlov explains the long latent period as follows:

The signal for food is not only the tone of 435 cycles, but also its duration. The animal has learned to react to a double stimulus—the combination of sound and time. When the tone begins, no saliva is secreted; but if an unexpected stimulus is added (light, noise, or a tactile stimulus), salivation at once begins. This is another instance of disinhibition, similar to the external inhibition of an extinguished positive conditioned reflex. We have here, according to Pavlov, a conditioned reflex of successive double sign. In a retarded conditioned reflex, the tone at first arouses inhibition in the cortex; but as the time for food approaches, the tonal stimulus changes its significance and arouses excitation, which is conducted to the salivary center, and secretion begins in anticipation of the food.

A related phenomenon is observed in the *trace* conditioned reflex. This type of conditioned response is established as follows. Some stimulus is chosen for the experiment. For uniformity of illustration, suppose that it is a tone of 435 cycles, and that an animal with no previous auditory conditioned reflexes is selected. The tone sounds for 5 seconds and is then discontinued; after 5 seconds of silence, food is presented. Soon the tone evokes no saliva; but during the silent period, salivation begins and increases in rate until the food appears. Then, gradually, as in the previously mentioned training procedure for the retarded reflex, the food is postponed, first to 10 seconds after cessation of the tone, then to 15, and so on, to a three-minute pause between tone and food. As the silent period, or period of no stimulation, is gradually lengthened, a corresponding lengthening of the latent period is observed.

In this case it is not the actual tone that is associated with the food, but rather the trace of the cerebral excitation aroused by the tone. This trace gradually fades during the pause, but it is still present when food is given. It is this trace that Pavlov believes is brought into con-

nection with the excitation aroused in the nervous system by the act of eating.

A striking characteristic of the trace conditioned reflex is its lack of specificity. A tone of 1,000 cycles presented after the formation of a three-minute trace of the tone 435 will also arouse a secretory response differing in no respect from the conditioned response to the 435-cycle stimulus. But it will be found impossible to train the animal to differentiate between traces of the two tones, that is, to salivate after tone 435 but not after tone 1,000. If the trace response to tone 1,000 is extinguished by withholding of the food, the secretory reaction to the trace of tone 435 will disappear also. In terms of Pavlov's theory, when the training tone is discontinued, the excitation, which has been confined during the action of the auditory stimulus to a small area of the cortex, escapes bounds and spreads or irradiates over the surface of the cortex as ripples spread out from the spot where a stone has been dropped into still water. A myriad of nervous connections are formed between points of the large area of the cortex excited through irradiation and the strictly localized salivary secreting center. This is the explanation advanced by Pavlov to account for the *initial* generalization of every newly formed conditioned reflex.

This concludes a brief survey of the method for establishing conditioned salivary reflexes in the dog and of the basic phenomena of conditioned reflex action revealed by the employment of Pavlov's technique. Certain important limitations of the method and of the theory of behavior based upon it must be noticed.

The Physiological Basis of "Psychical" Stimuli

As a consequence of the many years devoted to the investigation of the work of the digestive glands,⁽¹²⁾ the dog had become the standard animal for physiological re-

search in Pavlov's laboratories. He had, therefore, cultivated, through a great amount of experimentation, an intimate acquaintance with the behavior of this animal. During the study of the nervous mechanism of salivary secretion, it became necessary for him to decide what attitude to adopt toward the phenomenon of the psychical secretion of saliva. Salivation does not wait upon the stimulation of the buccal mucosa but is induced by sight and smell of food or even by the footsteps of the animal's attendant approaching the dog's kennel at mealtime. Pavlov eventually resolved to attack this special problem of anticipatory secretion from the physiological point of view rather than to neglect it as one falling outside the province of physiology. That is to say, rather than consider the psychical secretion of saliva as a topic properly belonging to the study of animal intelligence, he chose, instead, to consider it as a special case of reflex action. While salivation was observed to be constant and predictable when food was placed in the mouth, Pavlov observed, as had other physiologists, that secretion of saliva in anticipation of eating is capricious. He soon found, however, that if two conditions are rigorously observed, psychical secretion becomes as dependable as direct reflex secretion. When the dog salivates in response to changes in the environment associated with feeding, *food must always be given*. Since the dog reacts to each slight alteration of his surroundings, the *environment must be rigidly controlled* so that nothing will interfere with his reaction to the special signal indication that food is coming. Both cases of secretion, he concluded, are instances of reflex action; but in view of the fact that so many conditions must be satisfied in order to render psychical secretion dependable, he called this anticipatory secretion a conditioned salivary reflex, in contrast to the salivation that occurs when substances are placed in the mouth. This he called an unconditioned salivary reflex, because of the simple pre-

cautions necessary to stabilize it. Furthermore, the psychical or conditioned secretion of saliva depends upon the dog's education or experience with food-yielding environments. Conditioned reflexes are, therefore, temporary, and they vary from animal to animal. The unconditioned salivary reflex is a common possession of all dogs and is not altered by education. Since he found that the removal of the cerebral cortex abolished psychical secretion, Pavlov regarded the cortex as the special organ for the formation of conditioned reflexes. For this reason, his theory of the conditioned reflex seeks to explain behavior in its dependence upon the cerebral cortex; and for him, explanations of neural action involve two levels of the nervous system: the cortex and the subcortical centers, including brain stem and spinal cord. This simple neurological scheme is the basis of his theory of behavior.

The conditioned reflex theory is based, then, upon a legitimate and conservative modification of orthodox physiological method applied to a single vertebrate species, the dog. Behavior is studied by the measurement of the activity of a single effector organ, the salivary gland, under a variety of circumstances. But the salivary gland is only one of a number of effector organs involved in any given episode of behavior, and can give limited knowledge only of the range of adaptive response in the dog. Further, a theory of behavior based upon the study of but one animal species provides the psychologist or biologist with no basis for differentiating between those propositions that are valid for the dog's behavior only and propositions that hold true for animal behavior in general. Pavlov's theory in its present form is, therefore, a *special theory* concerning the control of a glandular effector by the brain in a particular species of animal exhibiting a complex pattern of behavior.

These limitations do not detract from the value of this unique approach to the study of behavior, but they should be duly appreciated by those who attempt to sublimate the

conditioned reflex theory into a nonexperimental doctrine for the purpose of *explaining away* rather than *inquiring into* the complexities of human behavior.*

Conditioned Motor Reflexes in the Sheep

For more than thirty years, Pavlov has directed intensive and systematic investigation of the dog's behavior by the conditioned reflex method. This effort has refined the method and simplified the theory based upon it. At the present time, both method and theory have come to be of practical interest to the psychologist and the physiologist.

An important extension of Pavlov's method is its application to the study of motor responses. It is now possible to make satisfactory quantitative comparisons of the conditioned motor reactions in several mammals. Although conditioned motor reflexes based upon the defensive flexion of the limb to the application of an electric shock were studied by the eminent Russian neurologist Bechterev⁽¹⁾ and his coworkers in the early years of the present century, no progress was made comparable to that achieved by Pavlov, mainly for the reason that the dog is an unfavorable animal for the study of reactions to noxious stimuli. Electric shocks seem to terrify the animal so that violent struggling occurs both to the conditioned stimulus and to the shock. Subsequently, other investigations of the motor reflex employing not only the dog, but man as well, were undertaken.^(7, 14) These investigations need not be reviewed in the present chapter, since they are researches aiming at the solution of special psychological or neurological problems and have not been continued as serious programs of experimental behavior study.

Beritoff^(2, 3) has most nearly approximated a systematic program of research; but in his case also, the investigation

* Cf. Chapter VIII and Chapter XII.

has not continued. He does, however, offer an interesting criticism of Pavlov's theory from the physiological point of view, based on his own brief study of the conditioned motor reflex in the dog.

The writer discovered, some years ago,⁽⁸⁾ in the course of an investigation of thyroid function, that the sheep is an excellent subject for behavior study and that it adapts itself easily to the requirements of the conditioned reflex method. With this animal, we have recently succeeded in verifying with considerable detail the principal behavior phenomena demonstrated by Pavlov and described above. This verification has been made possible by an ingenious method designed by O. D. Anderson for measuring the motor reaction to conditioned stimulus and electric shock. It was then found that the conditioned behavior of the goat, pig, dog,* and rabbit could be studied in the same laboratory and with the same experimental equipment employed in investigating the sheep.

Since our comparative studies of the conditioned reflex in sheep, goat, pig, and rabbit have enabled us to test Pavlov's theory in animals other than the dog, and since these studies have been made through the medium of the motor rather than the salivary reaction, it will not be superfluous to describe this further application of the conditioned reflex method as a preparation for a brief critical discussion of the essential characteristics of the method and of the logical framework of the theory.

In Figure 37 is shown the position that the sheep is taught to assume in the conditioned reflex experiment. During the preliminary training period, it learns to ascend an inclined platform and stand upon the table, where it

* In the case of the dog, however, the electric shock must be carefully regulated in strength so as to be just above the threshold for the motor reaction. A single-break shock rather than a brief series of shocks should be used. If this precaution is observed, the conditioned motor reflexes can be formed while the animal remains relatively quiet and docile between tests.

A LABORATORY FOR THE STUDY OF CONDITIONED MOTOR REFLEXES

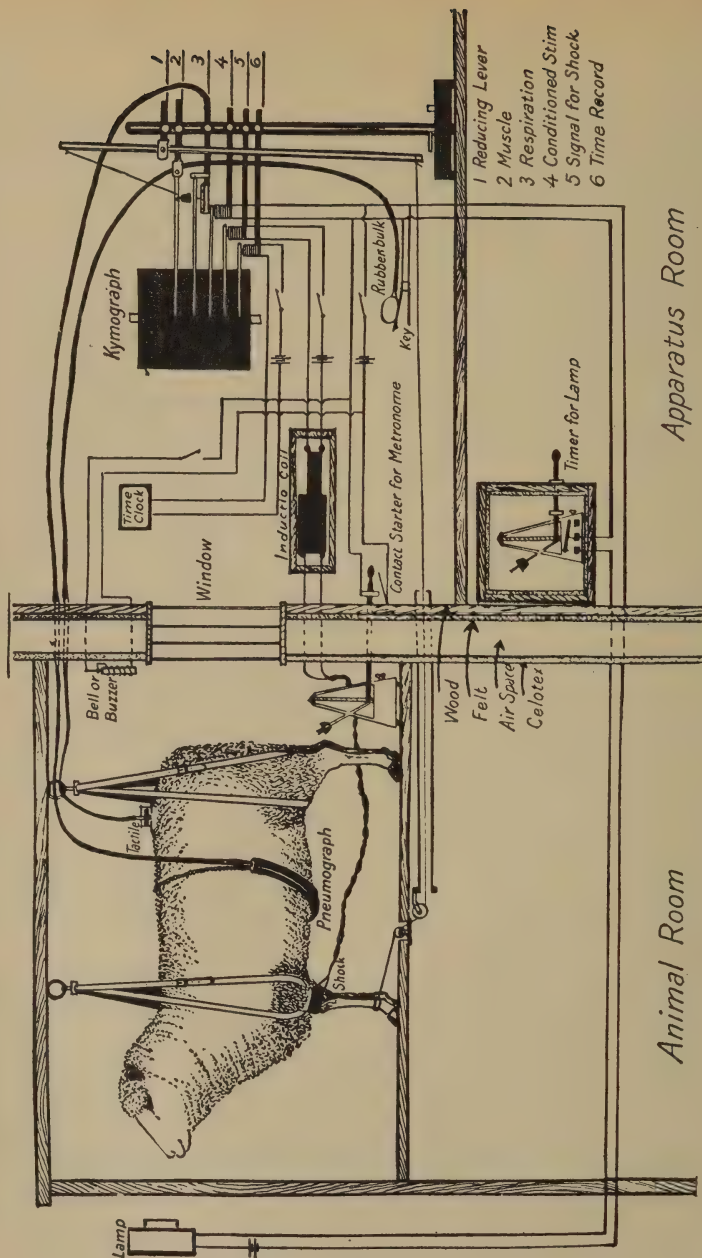


Fig. 37

eats from a bucket of oats. Since the sheep is a gregarious animal, it is necessary to have another sheep confined to a corner of the room. This "social" animal remains quietly in the corner but can be seen by the sheep on the table. Its presence, however, is an essential feature of the experimental method, for when it is taken from the room, the experimental animal becomes restless, the restless state being shown by repeated psycho-galvanic reflexes even when the animal is standing quietly.

In front of the sheep on the table is a baffle board with loud-speakers for the presentation of various auditory stimuli. The baffle board may also be used as a screen for the projection of various visual stimuli. Tactile stimulation is accomplished by cementing to different portions of the skin small brass cups. Each cup contains a rubber tambour bearing a disk with blunt metal points. When the tambour is inflated by pressure on a bulb, light contact is applied to the skin in any region desired. By the arrangements just mentioned, auditory, visual, and tactile stimuli can be presented to the sheep by the experimenter in the adjoining room. Wires wrapped on a leather bracelet fastened to the left foreleg are connected with the secondary coil of a Harvard inductorium, and a tetanizing shock passes through the skin when a pendulum switch closes the primary circuit. The shock commonly used in these experiments is that obtained with a coil separation of 4 centimeters when one dry cell is in the primary circuit. The response to this brief shock is a brisk flexion of the foreleg. A string fastened to this leg actuates the recording system in the experimenter's room. The movement of the leg operates the milled wheel of a Fick work accumulator and at the same time causes a writing lever to record the movement on the smoked paper of a kymograph. This arrangement is shown in Figure 38. Each movement of the leg revolves the wheel, and the total rotation of the wheel caused by repeated leg movements can be read di-

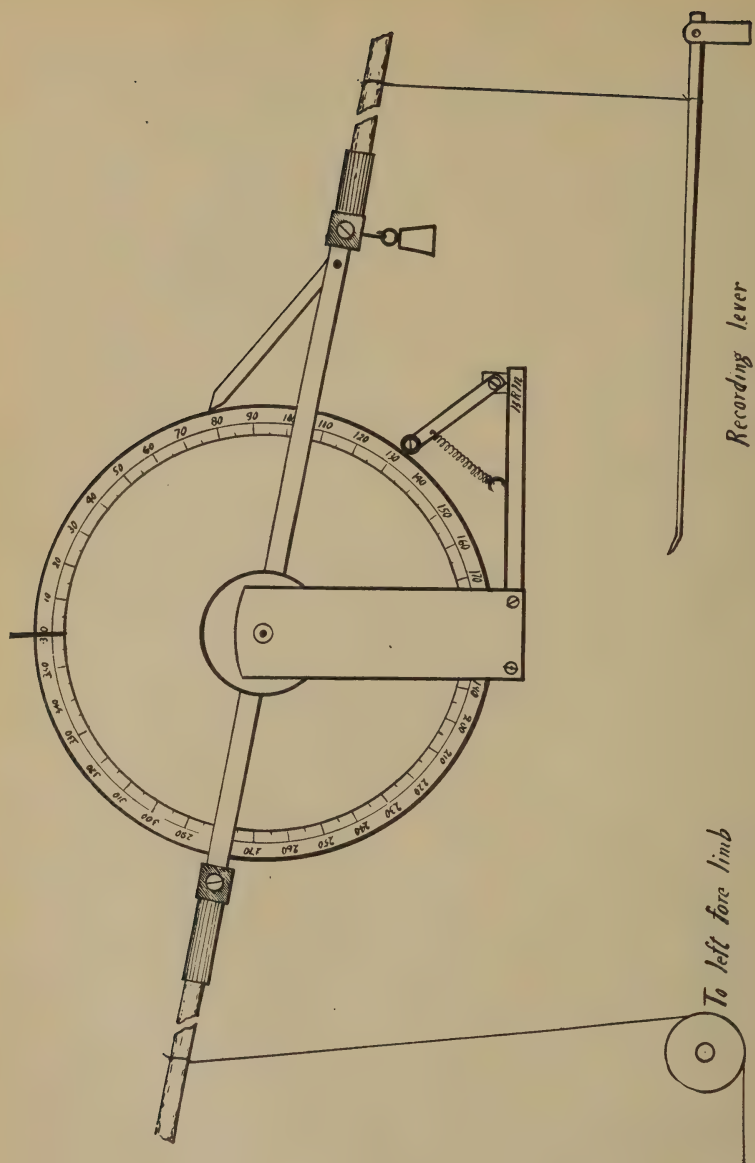


Fig. 38

rectly from the scale of the work accumulator. A quantitative estimate of the flexion reaction of the animal can thus be made, while at the same time a graphic record of the response is appearing on the kymograph.



Fig. 39.—Motor, respiratory, and psycho-galvanic reactions in the human subject to the sound of a buzzer for 30 seconds when always followed by a shock to the middle finger of the right hand. The top line records the movement of the stimulated finger as it rests on a tambour; the line below shows the respiration; the third line from the top records the level of skin resistance from the left forearm; and the three lowest lines give, respectively, the signal for the beginning and the termination of the buzzing, the application of the shock, and time in seconds. This tracing records the third presentation of buzzer followed by shock.

A pneumograph records the movements of respiration. Nonpolarizable electrodes placed astride the vertebral col-

umns in the lumbar region are in circuit with dry cells, a Wheatstone bridge, and a moving-coil galvanometer for the purpose of indicating the psycho-galvanic reflex during the conditioned reflex experiment. The movements of the galvanometer needle are followed by a pivoted metal pointer connected with a vertical writing lever. A horizontal line on the kymograph paper indicates constant skin resistance. A downward slope of the line signals the fall of skin resistance associated with the psycho-galvanic reaction. (See Figure 39.)

A conditioned motor reflex is easily established, as in the following example. A metronome beats once a second for five seconds, and then a shock is applied to the sheep's left foreleg. The metronome has no apparent effect upon the sheep's behavior (Figure 40), whereas the shock evokes

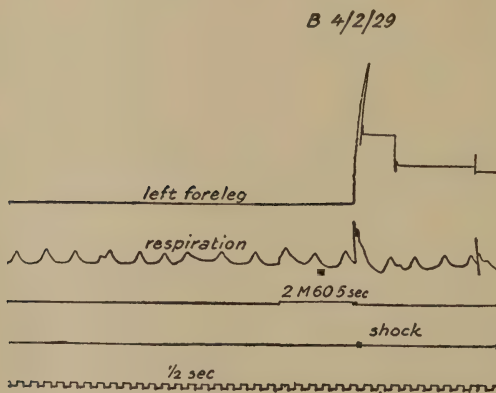


Fig. 40

a definite, brief flexion of the limb, the animal at once becoming quiet again. After four presentations of the metronome, beating 60 times to the minute and always followed after 5 seconds by the shock, the metronome stimulus causes a definite change in breathing (Figure 41). A light string attached to the head and connected with a myograph

lever demonstrates that this respiratory response is associated with a slight head movement. With the head movement and breathing change, the first conditioned psy-

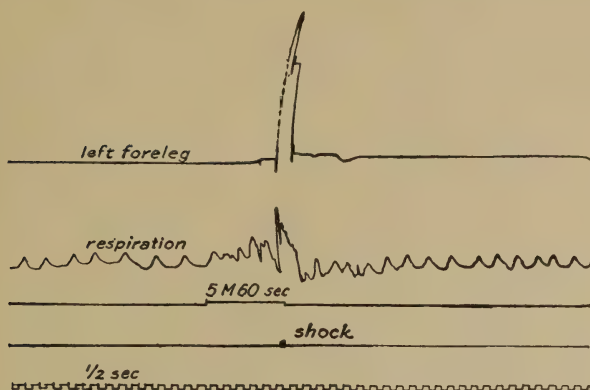


Fig. 41

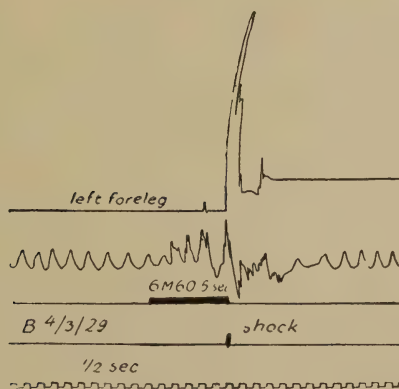


Fig. 42

cho-galvanic reflex appears. The first, small conditioned leg movement appears only at the sixth trial (Figure 42), and the fully established defensive reaction to the metro-

nome is not observed until the eleventh combination of metronome and shock (Figure 43). Other bodily functions are undoubtedly involved in the establishment of the conditioned motor reflex just described, even though it is diffi-

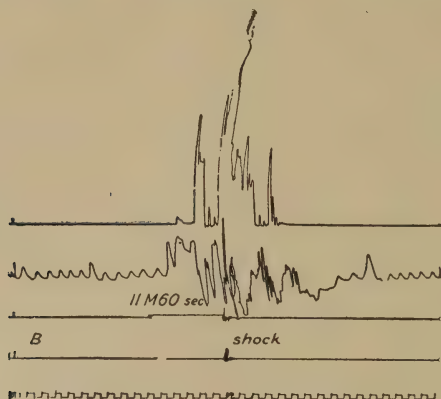


Fig. 43

cult to observe them. In man, for example, it is possible to demonstrate by means of the Keeler polygraph a conditioned cardiovascular response to the sound of a buzzer followed in 30 seconds by an electric shock applied to the finger. In the same experiment, it is quite simple to demonstrate the conditioned psycho-galvanic reflex also, by employing the technique described above.

The constancy of the conditioned motor reflex in the sheep is seen in Table X, where the metronome beating 120 times to the minute has been followed by the shock 505 times. This table illustrates the quantitative aspect of the method, the latent period elapsing between the beginning of the metronome and the first flexion movement being measured in seconds, and the sum of the flexion movements during the ten seconds of metronome stimulation being estimated from the total movement of the Fick accumulator wheel.

TABLE X
MEASUREMENT OF THE CONDITIONED MOTOR REFLEX IN SHEEP

<i>Conditioned Stimulus</i>	<i>Duration of Conditioned Stimulus</i>	<i>Latent Period</i>	<i>Magnitude of Conditioned Motor Reflex in Units of Fick Accumulator Wheel</i>
506 M120 *	10 sec.	3 sec.	25
507 M120	10 sec.	4 sec.	27
508 M120	10 sec.	3 sec.	23

* 506 M120 indicates the five-hundred-sixth sounding of the metronome beating one hundred and twenty times to the minute followed by an electric shock.

Positive, negative, retarded, and trace conditioned reflexes have all been established in the sheep upon the basis of the flexion reflex to the electric shock. We have also been able to demonstrate the phenomena of successive inhibition and positive induction under the conditions described by Pavlov. It is now possible to say definitely that the basic conditioned reflex phenomena described earlier in this chapter are not peculiarities of the dog's secretory behavior, but apply equally to the neuromuscular behavior of the sheep, an animal exhibiting a much simpler pattern of activity and possessing a different type of neural organization. A direct experimental test of the *general validity* of Pavlov's findings has here yielded unequivocal positive results.

Figures 44 and 45 show stages in the establishment in a sheep of a discrimination or differentiation between the sound of a buzzer and the sound of an electric bell. In Figure 44, the first record at the left shows the positive conditioned motor reflex to a buzzer after 111 combinations of buzzer with shock. The bell, never followed by the shock, at first gave a positive reaction, but this was extinguished by repetition. After a rest, the extinguished positive reflex to the bell was restored and at its forty-first application gave a positive reaction, but only three repetitions

were then required to extinguish it again. The completed differentiation between bell and buzzer in another animal is shown in Figure 45. The reflex to the bell is now definitely negative. Another precise differentiation in this

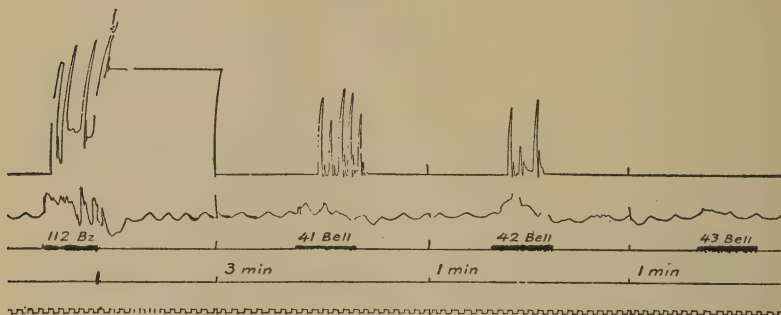


Fig. 44

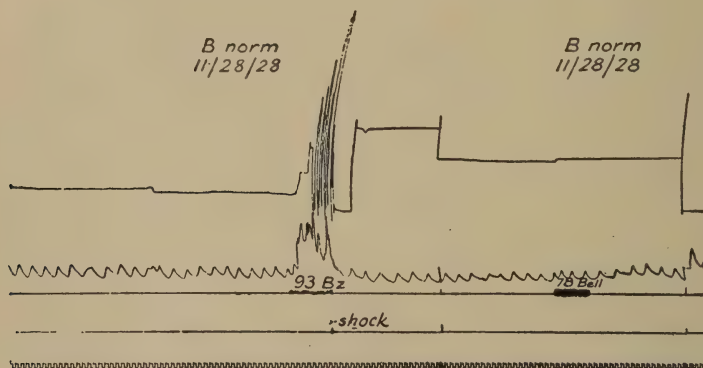


Fig. 45

animal is shown in Figure 46. The metronome beating 120 times to the minute is the positive conditioned stimulus, while the metronome beating 84 times to the minute, but never followed by a shock, is the negative conditioned stimulus.

Our recent experiments have convinced us of the value

of the conditioned motor reflex method in the comparative study of behavior.⁽⁹⁾ In the laboratory shown in Figure 37, and with the same apparatus, it has been possible to

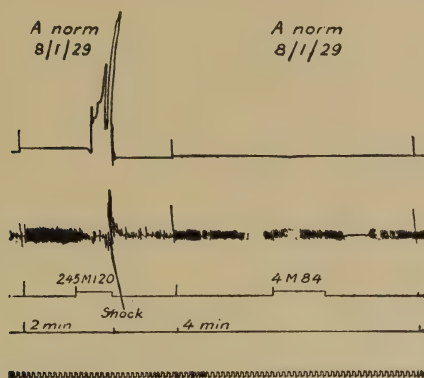


Fig. 46

compare the sheep, goat, dog, pig, and rabbit with respect to the number of trials necessary to establish a conditioned motor reflex to an auditory stimulus (a tone of 435 cycles per second). The conditioned reflex is established most rapidly in the pig, the leg movement in response to the tone appearing as early as the second trial. Its formation is progressively slower in the dog, goat, sheep, and rabbit. The conditioned reflex never becomes stabilized in the rabbit, and may appear in but 60 or 70 per cent of the tests. The newly formed reflex is more widely generalized in the sheep than in the pig, while in the dog the specificity of the new reflex occupies an intermediate position.

The attempt must now be made to characterize in a general way the method that has just been described and illustrated in detail.

Characterization of the Conditioned Motor Reflex Method

The chief characteristic of the method and its principal virtue is that the animal's environment is restricted and

simplified through training. This result is accomplished primarily through restricting the animal's activity. By careful education, it becomes accustomed to standing or sitting on the table of the experimental room, with locomotion prevented by a harness or collar. *In the absence of locomotion, the animal's capacity for self-stimulation is greatly diminished*, so that conditioned behavior is studied in a situation where spontaneous activity is much reduced or even absent. It is as if behavior were caused to flow in a narrow channel, and through stimulation the flow were retarded or hastened but seldom deflected in unexpected directions. The animal is made passive through training until it reaches a steady state of alert quiet, in which it responds only when stimulated. Behavior is thus broken up into episodes (conditioned reflexes) of relatively brief time-span, and between each two behavior episodes, the experimental subject relapses into quiet. In other words, the normal animal, in a strictly controlled environment where locomotion is prevented, *simulates* the behavior of the spinal cat or dog, whose behavior is simplified by the cutting away of the higher portion of the nervous system—so that the animal's environment is caused to shrink until it is coextensive with the body surface. In a vertebrate rendered passive by the destruction of its brain appear the highly individuated reflexes (spinal and decerebrate) that Sherrington, in particular, has investigated with so much success. Similar individuated responses to conditioned stimulus and shock are developed by the method for establishing conditioned motor reflexes. When the sheep, for example, has been well conditioned, the defensive responses to conditioned signal and shock—the flexion movements of the foreleg—are as precise and answer to the stimulus as definitely as in the case of the spinal dog or cat. There is an essential difference, however. In the early stages of training, the reactions to the shock and to the signal that precedes it are generalized and impulsive

to a high degree. The animal struggles in the harness as if trying to escape from the table, crouches, hangs on the straps; and this violent, general muscular activity may persist long (for many seconds) after the stimulus is discontinued. With increasing training, a gradual process of concentration and individuation supervenes. When the conditioned signal is presented, the sheep lowers its head, stiffens its forelegs, and then executes precise flexion movements of the leg that is to receive the shock. We have here an animal under normal conditions, with nervous system intact, that *through training* executes precise responses to stimuli closely resembling the highly specialized reflexes of the spinal animal. The strong impression of fixed relation between simple stimulus and specialized response that this experimental situation creates in the mind of the experimenter is the real motivation for the conditioned reflex theory; and in this theory of the origin of new behavior patterns, explanation is sought, through the use of the working concepts of spinal reflex action elaborated as a result of the very excellent experimental work of Sherrington, to account for the stereotyped and highly predictable behavior of the decerebrate animal.

However, recent experiments with the sheep demonstrate a fundamental difference between the field of action of the conditioned motor reflex and the field of action of the spinal motor reflex. When the sheep is standing quietly on the table with the head in the lateral position and the conditioned stimulus is presented, *the foreleg is not flexed*, but instead the animal struggles to correct the position of its head. Again, if the sheep is placed on its back and the conditioned signal is given, once again flexion of the foreleg does not occur, but instead all four limbs are stiffened and the animal attempts to lift its head. The response is a series of righting reactions rather than defensive flexion of the left foreleg. In other words, the flexion response built up by conditioning is the *focal point*

of a pattern of neuromuscular action involving, perhaps, the whole skeletal musculature.

Theoretical Considerations of Conditioned Reflex Methods

With regard to the details of Pavlov's theory, little need be said. It is only necessary to point out, first, that it is the outcome of a serious and practical intention to think of intelligent behavior in its dependence upon the central nervous system. The basic structure of this correlating mechanism is the same in all of its parts. It consists only of nerve centers, or regions of junction, interposed between pathways of conducting fibers. Therefore, those basic concepts, such as excitation, inhibition, irradiation, and so forth, that have been developed to explain behavior in its dependence on the spinal cord are adapted by Pavlov for integral parts of his explanation of behavior as dependent upon the brain. The concept of reflex action is regarded by him as the only basis for a truly physiological explanation of behavior, and he believes it necessary to extend the meaning of this concept rather than to formulate a new one, to account for the plasticity of action.

In Pavlov's thinking, each habitual action is referred to processes of excitation and inhibition of varying intensities, enduring for varying periods of time in localized regions of the cerebral cortex, which, for simplicity, is *imagined to be a uniformly extended sheet of nervous tissue*. He graphically represents behavior as plotted in terms of time and of brain space, but it is *imaginary space*.

In the second place, *it cannot be too strongly urged that the theory and the method can be divorced*. Every serious student of behavior must consider this method as a powerful and penetrating procedure for the disclosure of clear-cut facts in the fields of animal and human activity. Much of the controversial writing of the Gestalt psychologists is directed against the conditioned reflex,⁽⁶⁾ but these

authors fail to differentiate between the method and the theory that has originated in it.

It has already been shown that conditioned motor reflexes can be established in a number of vertebrate forms through very slight modifications of Pavlov's original procedure. At this point, it is necessary to attempt to answer a fundamental question. How does a conditioned reflex differ from a habit? This suggests related questions. How much of behavior consists of conditioned reflexes? Are conditioned reflexes established when an animal learns to escape from a maze? What essentially distinguishes the conditioned reflex method from other methods for the study of animal behavior?

It is obviously difficult to formulate adequate answers to these questions, but the attempt must be made if this chapter is to achieve its purpose. The method of the conditioned reflex is but one of the many techniques employed in the analysis of animal conduct. A detailed description of this particular method can be generally useful only if its scope and limitations are clearly set forth.

When we urged that the method here described could, and often should, be divorced from the theory of the conditioned reflex, the answer to our present question was implied. When an animal, after suitable training, is isolated in the experimental chamber and a signal intimating the approach of food or an electric shock is presented, its behavior in response to this signal is a conditioned reflex. But it is obvious that this behavior is in no sense unnatural or even unusual. There is nothing artificial about the conditioned reflex. It is a type of behavior elicited in a normal, domesticated animal that has not been mutilated nor anæsthetized nor placed under violent restraint. It differs from a maze habit only as regards the stage setting in which it appears; that is to say, its onset and cessation in response to a stimulus have been rendered so precise through careful systematic training as to invite quantita-

tive observation. However, a difficulty of definition at once appears. One must specify what aspect of the animal's behavior is quantitatively observed in the conditioned reflex situation. Surely, measurement of an animal's activity or even the graphic registration of it is not peculiar to Pavlov's technique. Thorndike's puzzle box method is quantitative. The acquisition by the cat of skill in escaping from the box is measured by the time necessary to operate the latch to the door, and the time decreases more or less steadily from the first attempt to the perfect performance after completed learning. A learning curve is then constructed from units of time and number of trials. Estimation of total motor activity during learning is rendered more precise in the maze or labyrinth method. The animal's activity is, in a manner of speaking, reduced from three dimensions in the puzzle box, to two dimensions in the maze; and in the maze, decrease in total activity in successive trials may be estimated in time taken to find the food, in distance covered in running through the labyrinth, or in errors made through entrance into blind alleys or retracing of the correct path. Once again, from time consumed, distance run, or number of errors, curves of learning may be constructed. Nor is graphic registration peculiar to the conditioned reflex method. In the first place, the larger portion of the experimentation in Pavlov's laboratories has been performed without benefit of a permanent record of the secretion observed. The amount of saliva is measured by the movement of colored liquid in the horizontal glass tube in the experimenter's room, and it is not considered essential that the secretion be registered by means of the electrolytic drop-recorder. In the second place, graphic registration can be employed in all of the familiar methods of behavior study. For example, the camera lucida attachment permits the observer to trace on a chart the rat's path through the maze. In the discrimination box, the animal may record its entrance into

either compartment by treading on a spring contact. Or again, the rat, cat, or horse learning to nose open a food box at a given signal can leave a permanent record on smoked paper, if an electric circuit is made when the lid of the box is lifted. The presentation of the signal associated with a filled food box can also be recorded by a signal magnet on the kymograph paper, and this record will show when the animal responds to the signal by opening the box, and how long it takes him to do so.

We were fortunate some years ago in observing the same sheep learning a simple T-maze and then, later, acquiring conditioned motor reflexes. From careful observation of maze habits and then of conditioned reflexes in the same animals, a very strong impression that habit and conditioned reflex are essentially identical modes of behavior was derived. Any acquaintance with the conditioned reflex that is derived solely from the printed page gives the false impression that this form of reaction is so localized and restricted that it lacks the robust, vigorous qualities of an ordinary motor habit. This impression is supported by the stress placed by Pavlov upon the extinction of the conditioned reflex. If food is not regularly presented after the signal for food is given, he tells us, the reflex grows weaker and will soon disappear. This phenomenon of extinction suggests to the reader's mind that the conditioned response is a fragile product of highly artificial laboratory conditions and, like the hothouse flower, cannot stand the rigors of the everyday environment. We are all familiar, on the other hand, with the inconvenience of old habits that refuse to disappear.

Then again, the various types of behavior that appear in the conditioned reflex setting and are described above are not easily identified with the commonplace activities of men and animals under ordinary conditions of living. Such terms as *induction* and *irradiation* when used by Pavlov to describe the activities exhibited by a mongrel dog

in his laboratory are not easily related to what dogs are observed to do in daily life. It may aid the reader to be reminded of a few simple instances of conditioned and unconditioned reflexes easily identified in human behavior.

When one is hungry and smells or sees palatable food, the flow of saliva into the mouth is clearly experienced. This is precisely the conditioned reflex with which Pavlov began his investigations. For some years, he referred to it as a *natural* conditioned reflex in contrast with the artificial reflexes established by associating the sound of a bell or metronome with the presentation of food. Later, he refused to make this distinction; but most psychologists still write of the dog's salivating when he hears the bell, when they wish to illustrate what is meant by the conditioned reflex—thus alienating the phenomenon from the realm of everyday experience. Dogs are not summoned to lunch by the ringing of a bell. One may obtain a convincing illustration of the conditioned motor reflex by recalling how he feels in the dental chair just after the dentist has said, "This may hurt a little." Again, try to recall your experience when the physician swabs your arm with alcohol just *before* he plunges the hypodermic needle into the skin. Think, again, how you felt just before an inevitable collision was to occur between the car you were driving and another that had suddenly backed out of a driveway. If the collision that seemed inevitable was avoided, try to remember how you felt for some moments *afterward*. In making the self-observations just suggested, another important point appears. Your experience in anticipating food differs from your experience in eating it. Your discomfort when the dentist is actually hurting you is certainly quite other than your anticipation of being hurt. The nervous tension of waiting for the hypodermic needle to pierce the skin contrasts as black against white with the ridiculously small discomfort of the actual prick itself. Yet in all of these cases, the conditioned reflex type of

behavior is exhibited during the anticipatory period, whereas the time of realization is the time during which behavior is of the unconditioned type. However, this vivid contrast between one's experience during conditioned behavior and then during the unconditioned reaction is not always in evidence. For example, although the athlete toeing the starting line for a sprint will sometimes "jump the gun," his usual behavior consists of building up more and more tension at the verbal commands preceding the firing of the pistol.*

One may say, in general, that *the positive conditioned reflex is not a replica of the unconditioned reflex that follows it*, as is often asserted by psychologists. The misunderstanding upon which the identification of conditioned and unconditioned reflex is based is easily comprehended when one remembers that Pavlov selected only a single sample of the dog's total behavior in the conditioning situation for study: the quantity and rate of salivary secretion. Since the dog salivates at the signal for food and again when he eats, the only response quantitatively observed is obviously the same before and during mastication. Pavlov has stressed the identity of conditioned and unconditioned salivation in pointing out that when weak acid is poured into the mouth, the unconditioned secretory response is a watery saliva in relatively large amount. A signal preceding the introduction of acid into the animal's mouth arouses, also, a copious flow of watery saliva. Eating causes the secretion of a more viscous saliva, and so does the expectation of food.

The salivary response is, however, *but one sample* of the highly intricate behavior of the dog in response to the signal that food is coming. A characteristic attentive posture is assumed, breathing is modified, and so forth. How

* In the conditioned reflex laboratory, the sheep, goat, and pig regularly "jump the gun," that is, they respond by movement rather than by a tense attitude when the conditioned motor reflex is well established.

unlike this rigid posture when he expects food is the dog's greedy plunging and vigorous gulping of the food when he eats! Although the secretory reaction of expectation is essentially identical with the secretory response to the eating of the food, the conditioned *motor* alimentary response differs radically from the unconditioned *motor* alimentary reflex. The two highly integrated acts of expectation and eating are quite dissimilar except for the common component of salivary secretion.

Why, then, does the behaviorist assume identity of conditioned and unconditioned reaction? It can only be to support, *in the face of the facts*, a simple "pathway" or "bond" hypothesis of learning. Once again, let the reader remind himself that no physiologist or psychologist is committed to the acceptance of Pavlov's intricate theory of the conditioned reflex or to any of the numerous oversimplifications of the theory propounded by psychologists when he employs the method of the conditioned reflex for the purpose of disclosing definite facts concerning behavior. No clinician feels it necessary to espouse a particular theory concerning the causes of hypertension because he employs the sphygmomanometer to detect the abnormally high blood pressure indicative of this condition. Even in physiology, this essential independence of method and theory derived from its use is not always as clearly recognized as it should be. For example, one may employ Lapicque's technique for measuring chronaxie without accepting the complex theory of neural action that he has derived from the varied applications of his method of measuring excitability.

The following observations of the behavior of the sheep convinced us that maze habit and conditioned motor reflex are fundamentally equivalent one to the other. A simple conditioned motor reflex was established by the combination of the ticking of a metronome with the application of an electric shock to the left foreleg. The sound of

the metronome soon induced vigorous flexion of this limb. When the response became quite stable, a rest period of two years intervened before the metronome was heard again. After this interval of no practice, the ticking of the metronome at once evoked vigorous flexion of the left foreleg. In another experiment, the sheep learned to escape from a modified T-maze in order to join the flock and obtain food. In this case also, the maze habit was retained after a rest period of two years, but not so perfectly as was the conditioned reflex; that is, some hesitation was shown in the choice of the correct path at the alleys' intersection. The wrong alley was chosen in one case, although the animal ran the maze as if thoroughly familiar with it. Behavior prior to entering the maze is an integral part of the maze habit. Our sheep regularly ran to the starting box of the labyrinth when the door from the barn into the feeding compartment was opened. In many cases, when the door was opened, an animal would come to the door and push past the observer into the maze. In one instance, an ewe with a newborn lamb left its offspring and ran into the maze, performing the difficult double-alternation habit without regard to the lamb's loud bleating. In the conditioning experiments, the sheep is led on a leash from the barn to the conditioned reflex laboratory, about fifty yards distant. The trained sheep tugs at the leash, when released from the barn, and leads the experimenter to the laboratory room, where it voluntarily climbs the platform onto the table. When the conditioning problem becomes too difficult, as in the case where a shock follows the metronome ticking 120 times to the minute, but no shock follows the sound of the metronome ticking 100 times to the minute (a difficult discrimination), the animal may suffer a nervous breakdown similar to the "experimental neuroses" observed in Pavlov's dogs under like circumstances. The first intimation of such an acute nervous disturbance is that the sheep on leash, upon being released

from the barn, tries to lead the experimenter away from the conditioned reflex laboratory, and when forced to go there, tries to avoid entering the experimental room.

If the sound of the metronome is the signal of an approaching shock to the foreleg, this limb will be vigorously flexed while the metronome is ticking. If the shock is discontinued and the metronome is sounded again and again, at intervals of a minute, the defensive movements of the leg die out, and finally the sheep remains quietly standing on the table while the ticking continues. If the animal is taken from the laboratory and brought back again, after a few hours, the conditioned reflex to the metronome will reappear, but now it dies out more quickly if the electric shocks are not given. This experiment illustrates the extinction of the conditioned reflex to the metronome when it is not reinforced by the unconditioned reflex evoked by the shock, and the spontaneous restoration of the extinguished conditioned reflex during a rest period.

Similar phenomena were observed in the simple T-maze when the position of the blind alley was reversed and the alley that formerly led to the food became the *cul-de-sac*. When sheep that had learned the T-maze were caused to learn it again with the *cul-de-sac* reversed (three errorless trials being taken as the criterion of completed learning), the animal's behavior in avoiding the new blind alley that just previously had led to the food strongly resembled the extinction of the flexion response to the metronome when the shock no longer followed. (Table XI). The blind alley was entered less and less often as one trial immediately followed another, until the error score fell to zero. Then the sheep rested until afternoon. When it was again placed in the maze, the old habit that had been suppressed was found to be restored. The sheep again entered the *cul-de-sac* (as is indicated by the 2 errors of trial 6), just as the sheep after a rest once more flexed its leg to the

sound of the metronome that was no longer a signal for a shock.

TABLE XI

SHEEP RELEARNING A SIMPLE MAZE WITH THE POSITION OF
THE *Cul-de-sac* REVERSED

<i>Time of Day</i>	<i>Trial</i>	<i>Errors</i>	
5:58 A. M.	1	33	} —Errors due to entrance into <i>cul-de-sac</i> that previously had led to the food.
	2	20	
	3	3	
	4	0	—Extinction of the old maze habit.
	5	0	
(Tests interrupted.)			
4:45 P. M.	6	2	—Spontaneous restoration of the extinguished maze habit.
	7	0	
	8	0	
	9	0	—Completed learning of reversed maze according to the arbitrary criterion of three errorless runs.

Finally, conclusive evidence as to the full-bodied, robust character of the conditioned motor reflex was obtained by observing conditioned reflexes in the sheep *outside of the laboratory*. The following experiment of O. D. Anderson is representative of a number of tests. The attempt was made to establish a conditioned motor reflex in which the presentation of food was the signal that an electric shock was soon to be applied to the shaved skin of the left foreleg. A tin dish containing oats was mounted on a swivel arm so that it could be concealed behind a screen. By a pull on a cord in the adjoining room, the food dish was swung out from behind the screen and came to rest in front of the animal. At first, the sheep nibbled the oats whenever the dish was presented. Then the experiment was begun. The food was presented for 15 seconds and then the shock to the foreleg was given. Soon the sheep would lower its head to eat but would arrest this movement, brace itself, and begin flexing the foreleg. Finally, the first appearance of the food dish at once induced vigorous flexion of

the left forelimb with no indication of the original feeding reaction. When this new reflex was established, a test was conducted with the small flock of sheep in the barn. A bucket of oats was placed in the center of the floor, and around it the animals clustered trying to get a share of the food. The sheep for which oats meant electric shock circled round and round the bucket but carefully avoided approaching it even when alone in the barn with the oats.

When a positive tactile conditioned reflex has been formed in the sheep by stimulating a spot over the ribs by means of the tambour device previously described and following this stimulation with a shock on the skin of the foreleg, and when a spot about three inches distant from this one is stimulated but no shock is given, a differentiation or discrimination of the two skin areas is established. The animal will now flex the left foreleg when the one spot over the ribs is stimulated, but will not flex the leg when the adjacent spot is touched, although it may turn its head toward the "negative" spot. This latter response is a negative or inhibitory conditioned reflex (although the animal gives a characteristic motor reaction). These acquired motor responses may be elicited in the barn if the experimenter taps the appropriate skin areas over the ribs with the finger. It has also been repeatedly observed that when standing in an unfamiliar laboratory room or in the barn, the sheep will flex the foreleg in response to the sound of the metronome, if this reflex has previously been formed in the usual way.

It will be remembered from the previous description of Pavlov's findings that the conditioned salivary reflex is diminished or suppressed by an unusual or unexpected stimulus even when the intensity of this new agent is very small. This phenomenon was named "external inhibition" and was said to be due to the prepotency of the dog's orienting reaction to any novel sensory disturbance. In plain language, the dog is so curious that he is easily dis-

tracted. It is probable that Pavlov has exaggerated the influence of distraction on the conditioned reflex. He claims that a stimulus which the experimenter *cannot detect* may measurably reduce the magnitude of a newly formed reflex in a crucial test and thus spoil an experiment for which it has taken months to prepare. In effect, Pavlov here removes his theory from the test of experiment, since any reflex of less than the predicted magnitude may thus be explained as due to the influence of a distracting agent beyond the experimenter's power to detect and hence to control. As a matter of fact, tests in our laboratory have failed to confirm the great potency of external inhibition even in the dog. The sheep is almost immune to distraction. (Some instances of external inhibition in the sheep have been observed: for example, when the animal is performing before an audience.) Pavlov's unfortunate emphasis on external inhibition has been an important factor leading to the confusion concerning the nature of the conditioned reflex. If it is so susceptible to slight disturbances of the environment (such as small changes of illumination, and the like), one may conclude that it must be far more fragile than an ordinary habit, and must fundamentally differ from it. Our results show that the formation of the maze habit is far more seriously disturbed by distraction than is the establishment of the conditioned motor reflex in the sheep. Both sheep and goats will pause in running the maze to investigate dead leaves blown about by the wind; but in the conditioned reflex laboratory, they will ignore the rattling of a box of dried peas, the swinging of a large paper disc, or even unexpected tactile stimulation during the formation of a conditioned reflex to the sound of a buzzer. They will acquire the new reflex as rapidly under distraction as under the usual uniform environmental conditions.* Not only is the motor habit that leads the

* Experiments of O. D. Anderson.

animal through the maze or to the correct compartment of the discrimination box essentially similar to the habit of flexing the leg when the approach of an electric shock is signalled, but the avoidance of the *cul-de-sac*, or of the compartment of the discrimination box where no food is to be found (or where an electric shock awaits it), is also the same kind of motor habit as is exhibited when the animal learns not to flex the leg when the signal for no shock is given. Avoidance of a *cul-de-sac* in the maze or one of the compartments in the discrimination box is the equivalent of Pavlov's negative or inhibitory type of conditioned reflex.

To summarize what has just been said, the conditioned reflex method is characterized neither by its emphasis upon quantitative observation nor by its provision for graphic registration of response. The new patterns of activity that are built up through the use of the conditioning technique differ in no fundamental respect from the habits acquired by an animal in the discrimination box and maze. The conditioned reflex, whether motor or secretory, is just a habit.* How then shall we answer the question: What

* *Habit* is a word borrowed from common speech that the physiologist should be reluctant to use as a technical term because it is his business to inspect the functioning of the organism in detail in order to decipher its pattern of activity. *Habit* ordinarily implies acquired modes of movement, posture, and speech. But the organism can form habits of temperature regulation, urinary secretion, pupillary dilatation, and so forth. An instance of what is meant is recounted by Cannon in describing the altered behavior of cats from which the sympathetic chains had been removed. These cats, when placed in a cold room, exhibited a falling body temperature. The decline in temperature was arrested from time to time by shivering. One animal, however, survived without a sympathetic system for a year. "During the year that had elapsed . . . the animal appears to have become accustomed to reliance upon shivering as the main protection against a temperature fall. On being placed in the cold room, it very soon began to shiver vigorously, and by so doing prevented a marked drop in temperature and, indeed, managed to maintain its normal temperature level." (4:264.)

Conditioned reflex is a better term than *habit* because it is technical and not colloquial. One may refer without ambiguity to conditioned dilatation of the pupil, conditioned temperature regulation, conditioned

essentially distinguishes the conditioned reflex method from other methods for the study of animal learning?

Perhaps it is the point of view adopted by the investigator that really characterizes the conditioned reflex method, rather than selection of apparatus or details of experimental procedure. In seeking to contrast this method with the methods commonly employed by the comparative psychologist, it must be remembered that it originated in the physiological laboratory as the consequence of an obstacle encountered in an investigation of the nervous mechanism of salivary secretion, as has already been related. In view of this historical fact, it is reasonable to place the conditioned reflex method among the other experimental resources of the physiologist. The point of view, as behavior is concerned, characteristic of the investigator of the conditioned reflex should be the physiological one. The fundamental task that must be faced is the determination of a reasonable division of labor, in the study of animal conduct, between psychologist and physiologist; and this task must now be attempted.

Every experiment in physiology begins in the same way. The investigator exercises his knowledge and ingenuity to the full in trying to stabilize the living system upon which the experiment is to be performed. The chemist, working with pure reagents, brings them to react only when every surrounding condition, such as temperature, atmospheric pressure, and the like, is quantitatively known and under control. The physiologist cannot actually control the complex forces at work in the living system, but he can do his best to stabilize it while under observation and, in so doing, greatly simplify the task of disentangling the threads of this intricate living tapestry. Most diverse expedients have been adopted thus to bring the living protoplasm to the desired state of neutrality. Vivisection and the use of

urinary secretion, or conditioned contraction of skeletal muscle (or movement, posture, or speech).

drugs are classical examples. If one wishes to investigate the intimate nature of muscular contraction, a basic level of activity in the muscle must be achieved before the actual process of contraction is observed. Every student of elementary physiology is familiarized with the nerve-muscle preparation, because from the behavior of this simple fragment of the vertebrate organism, the basic facts concerning muscular action have been derived. When its motor nerve is severed, the skeletal muscle is at once completely paralyzed. It cannot contract unless stimulated directly or indirectly through its severed nerve. When the muscle is paralyzed, it is, however, not dead, but has relapsed into a state of complete quiet in which its metabolism (the sum total of chemical changes occurring within it) maintains a remarkably uniform level. Each time that a stimulus is applied, the muscle responds by the execution of a brief contraction and relaxation, the simple muscle twitch.

Experimental analysis has shown that each and every muscular activity, whether of posture or of movement, may be resolved into a sum of simple muscle twitches. Other organs have, by vivisection, been removed from the organism in order that their function might be stabilized—the better to analyze their essential activity. For example, the living kidney has been isolated, a flow of blood through it maintained, and normal samples or urine collected from its duct. The transection of the spinal cord, in like manner, reduces the “spinal animal” to a state of paralytic quiet in which the spinal cord, severed from its brain, is roused to activity only by the application of a stimulus to a receptor or afferent nerve. The response in answer to this stimulus is called a “spinal reflex” and is a conveniently studied fragment of behavior elicited from an animal stabilized through vivisection. The animal whose behavior the physiologist wishes to fragment may be most conveniently brought to a state of neutrality through the use of an anæsthetic, or, for the study of secretion, the same animal

may be reduced to a state of even more profound rest by the injection of curari, which completely paralyzes its skeletal muscles.

The essentials of a physiological experiment, as shown by these examples, are two. A *definite sample* of living activity (contraction or secretion) is selected for quantitative observation. The tissue or organ from which the desired response is to be obtained through stimulation is *stabilized* or neutralized in order to give a base line for a quantitative estimate of the performance.

Stabilization and sampling characterize not only experimental physiology but the practice of medicine as well. The chief function of the hospital is to stabilize the life processes of the patient in order that samples of his vital functions may be selected for careful observation as a basis for diagnosis. Upon entering the hospital, the patient is put to bed. In a surgical case of goiter, for example, daily samples are taken of basal metabolism, body temperature, pulse rate, respiratory rate, and differential blood cell count. In each case, the observations are recorded in quantitative terms. Only when these values show a mutual relation that experience indicates to be favorable does the surgeon proceed with the operation.

From the detailed description of the conditioned reflex method given above, it will be seen that in this method the two criteria of the physiological experiment are realized. The animal's spontaneous activity is reduced to a minimum through training, with the result that it is brought to a state of alert quiet. Then the conditioned reflex (defensive or alimentary) is elicited in response to a measured and controlled stimulus. This reflex during its occurrence is studied through sampling, and each sample is estimated quantitatively. In the conditioned motor reflex established upon the basis of the defensive reaction to an electric shock, the following samples of organic function have been successfully studied: the estimated magnitude of the total

motor response during conditioned and unconditioned stimulation; the pneumogram, showing rate and form of the breathing response; the galvanic skin reaction (psycho-galvanic reflex); and the pulse rate.

The reader may at this point ask a simple but disconcerting question: What are you going to do with these samples when you get them? It must be confessed that no satisfactory answer in general terms can be given at present. An example from an actual experiment will show, however, that the sampling is not labor lost. In our experiments with the T-maze, we were puzzled to discover that sheep and goats, in spite of their striking differences in general behavior with which everyone is familiar, were equal in their ability to learn. Moreover, they formed conditioned motor reflexes with equal facility, about eight combinations of signal followed by shock preceding the first anticipatory leg movement.

It is generally assumed that the goat is more intelligent than the sheep. It is less timid—seems more alert, more curious, and, in general, more reactive. When first placed in the maze, it spends much time on its hind legs attempting to peer over the walls of the alleys. In the conditioned reflex laboratory, it seems to show great irritability and resentment. Often, a single tick from the metronome, when this is the conditioned stimulus, causes the animal to raise its foreleg and to hold it, trembling, in this position for many seconds. The sheep's response to the same stimulus is usually nothing more than an orienting movement of the head, a small, perfunctory movement of the foreleg, or a slight shifting of weight. At the shock, the sheep may briskly flex the leg or even jump; but the goat will, in addition, belabor the supporting beam with its horns or bite at the electrodes. The squeals and grunts of the pig, accompanied by struggling, at the signal and shock also suggest most active resentment. When the galvanic skin reaction is recorded during the extinction of the conditioned

reflex in the sheep, the fall in electrical resistance of the skin is found to decrease as the conditioned leg movements decrease with repetition of the conditioned stimulus without the electric shock. The leg movements and the fall in skin resistance disappear at the same time. In the case of the goat, however, vigorous galvanic skin reactions are elicited long after the defensive leg movements have disappeared. Since the galvanic skin reaction appears to be mediated by the sympathetic nervous system, and since Cannon ⁽⁴⁾ has shown that it is this system, together with the adrenal glands, that prepares the body to meet the stresses of an emergency, it can be seen that the emotive character of the conditioned defensive reflex is especially marked in the goat as compared with the sheep. To state the matter crudely, the sheep is a cold-blooded learner, while the goat is a hot-blooded learner. This distinction in the galvanic skin reaction, associated with the defensive motor habit in the sheep as compared with the goat, brings the student of behavior into concrete relation with the problem of temperament or personality-type in its bearing upon learning, and suggests specifically the influence of the sympathico-adrenal function upon the formation and general character of the defensive conditioned response.

If the reader be willing to accept the essential identity of motor habit and motor conditioned reflex, the maze method (and similar ambulatory methods) can be distinguished from the conditioned reflex method quite simply, as follows. The two methods present the habit that is being established through training in two distinctive stage settings. When the maze method is employed, the habit is dramatized in such a way that the experimenter's attention is focused upon the outcome of the animal's activity. The animal is going somewhere, and the investigator is interested in how soon it will get there and how efficiently, that is, with how little unnecessary exertion. The investigator is also interested in noting the rapidity with which

it improves through practice, and in comparing the experimental animals with regard to their proficiency in problem solving or learning. The experimenter sits in judgment and evaluates their intelligence, sorting out the bright animals from the stupid, and so forth. The method is an output method. It limits the experimenter's inspection of function to the altered relation between organism and environment that results from the exercise of the function. The animal starts at *A* and stops at *B*. Charting its path and determining how much time was spent in transit is supposed to throw light upon the operation of the living machinery (the learning process) that translated the organism from *A* to *B*. The curve of learning is the typical result of the use of the maze method and of related methods.

In the conditioned reflex setting, the investigator is induced to focus his attention upon the details of the performance as it transpires. In imagination, he looks beneath the skin and reconstructs from the graphic record of the conditioned reflex the shifting patterns of activity going forward in the hidden tissues of the animal.

Pavlov says: ^(11:222)

If we could look through the skull into the brain of a consciously thinking person, and if the place of optimal excitability were luminous, then we should see, playing over the cerebral surface, a bright spot with fantastic, waving borders constantly fluctuating in size and form, surrounded by a darkness more or less deep, covering the rest of the hemispheres.

This, however, is only a portion of the larger picture that the physiologist tries to imagine when samples of the activity of the various organs record themselves on the moving paper of the kymograph or photographic film.

Whereas the investigator employing the maze is interested in the form of the curve expressive of increasing familiarity with the maze, the experimenter attempting to analyze acquired modes of behavior by means of the con-

ditioning technique asks only: "Can the animal establish a positive or negative conditioned reflex to a given stimulus?" If so, he wishes it to be stabilized as soon as possible in order that the intricate details of its functional composition can be determined. Each new habit, for the physiologist, penetrates deep within the organism. The simple flexion of a limb in anticipation of a shock involves not only brain and muscle, but skin, spleen, adrenals, liver, lungs, and kidneys. In fact, from the physiological point of view, every tissue is suspected of changing pace and direction of function with each adjustment of the organism to change in the external environment. The physician knows only too well that brain and muscles do not operate in isolation. How else can he explain to himself the manner in which the shock of an injury, or even worry over an ethical problem, may induce the growth of a goiter?

A further important issue suggested by the conditioned reflex method concerns the capacity of the brain for effecting adequate adjustment to a difficult environmental situation. Shock and no shock can be associated with closely similar stimuli to auditory, cutaneous, or visceral receptors, and the limits of sensory discrimination can thus be determined. Here again, interest is centered, not upon how rapidly two tones are differentiated, but only upon whether or not a stable discrimination can be achieved. Once a differentiation is established, the effect upon it of drugs, lack of sleep, defective diet, endocrine disturbance, and the like, may be determined with the precision necessary to make the knowledge of use in medicine.

Pavlov has also clearly demonstrated, by the employment of the conditioned reflex, a type of enduring nervous disturbance that may be experimentally produced if the demand for delicate discrimination exceeds the capacity of the animal's brain to effect it. In such cases, a nervous bankruptcy occurs, and a condition supervenes that bears striking resemblance to nervous breakdown in man. These

studies further broaden the horizon viewed by the physiologist interested in analyzing behavior.

It is now necessary to discuss the use of the method of conditioning in the analysis of the more intricate modes of behavior variously designated as "the higher forms of learning," "insight," "intelligent behavior," and "planned action." The physiologist must be agnostic in his attitude toward the application of the conditioning technique to these most highly integrated forms of behavior. Only the future can decide the limits of Pavlov's method. It seems likely, however, that the "stabilizing and sampling" frame of mind on the part of the experimenter directs his attention away from the more labile and complex behavioral adjustments in which the psychologist is primarily interested. One must be reminded, however, of the years that elapsed before the physiologist was able to demonstrate by refined mechanical and electrical methods that the simple muscle twitches exhibited by the nerve-muscle preparation are the building stones out of which the various animal postures and patterns of movement are constructed.

In conclusion, it may be said that if the reader desires to understand theories of behavior, he must know the facts upon which such theories are based. Indeed, he must do more. He must acquire a clear conception of the various methods or procedures that have been employed to disclose the facts upon which the theories rest. A skilled craftsman must possess, in addition to manual dexterity, a sound, practical knowledge of the appropriate tool for a given task. The enterprise of experimental behavior study makes similar demands. The serious student of behavior is puzzled by some activity of a particular animal, or he is skeptical of a current hypothesis to account for learning. In either case, he desires to satisfy his curiosity or clarify his own thinking, and he decides to experiment. What method shall he adopt in analyzing the bit of behavior that has attracted his notice, or in putting the doubtful

hypothesis to the test of experiment? The usefulness of a book such as this is to be found in the disquieting effect that it exerts on the reader's mind. Many theories of behavior are presented. If he is critical, he cannot accept them all. Many methods for the experimental analysis of behavior are described. What are their limitations and defects? Which one would he select if he were to attempt to solve some problem that may have occurred to him in reading this book?

The aim of the present chapter has been to describe in detail the characteristics and uses of one particular tool in the workshop of the comparative psychologist. This tool is the conditioned reflex method.

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CHAPTER X

Learning

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Introduction

TO learn means to modify one's reactions through experience. This is a short, concise definition of *learning*. It is so short and concise, in fact, that it needs a word of explanation.

Professor Stone has distinguished between learning and another type of development—maturation (see Chapter III). We quite agree with this distinction and shall, therefore, turn to another point. We wish to make clear that in the term *to modify one's reactions* no implication of deliberation is intended. The human being or the lower animal may or may not deliberately modify his reactions. That is a question which cannot be discussed in generalities. It can be considered only with reference to each specific instance of modification.

A second point we wish to emphasize is that by the term *experience* we do not intend to commit ourselves to any implications concerning consciousness. By the term *experience*, we mean only the mark left upon the organism by the interplay between the organism and its environment. Some of this interplay may involve consciousness; probably a large percentage of it does not. Here again, we cannot deal with generalities, but, in so far as the question

of consciousness can be discussed at all, it must be discussed with reference to specific instances.

In our definition we have spoken of learning as the process of modification. Now let us draw attention to another phrase that is commonly used, namely, *learning ability*. By this term is meant the ability the organism possesses to make the modification. That is, when we see the process of modification of reactions through experience taking place in an organism, we infer that the organism has a certain degree or kind of ability that makes this process possible. The possible nature of this inferentially known ability is discussed, in certain specific respects, at least, in Chapter XIII by Professor Tryon. Also, Professor Tolman in Chapter XII discusses the theories of learning, which are attempts to understand how this learning ability or abilities operate.

Distribution of Learning Ability in the Phylogenetic Scale

The ability to learn is preëminently a characteristic of the normal human being. However, this capacity is also present, in varying degrees, in animals that man has placed below himself in the phylogenetic scale. In fact, there is evidence which indicates that all species (from the unicellular animals upward) are capable of learning. Of course, all species have not been investigated in this connection, but various investigators have sampled different species along the scale to such an extent that we are justified in making the statement.*

To be sure, the extent to which modification of reactions

* The reader who is interested in this question will find it of value to examine the following references for indications of learning in animals that rank lower in the phylogenetic scale than those discussed in this chapter:

Jennings, H. S.: *Behavior of the Lower Organisms*. New York: Columbia University Press, 1906.

Smith, Stevenson: "The Limits of Educability in *Paramecium*," *Journal of Comparative Neurology and Psychology*, 1908, Vol. 18, p. 499.

takes place varies widely in different species. One would not expect a paramecium, for example, to be able to learn to solve a problem in calculus; but then, a paramecium does not meet calculus problems in his environment. However, if by some decree of an experimenter he were required to do so or else give up his earthly existence, he would be forced to the latter fate. In other words, the relatively simple organization of the paramecium does not permit him to learn this relatively complex problem. To put this matter in more general terms, we find that there is a rough correlation between the position of each of the various species in respect to the rest in the phylogenetic scale and the complexity of the problems that it is able to learn to solve.

There are many factors that prevent this correlation from approaching perfection. One of the outstanding of these is the great extent to which instinctive behavior is predominant in some types of animals, particularly the insects. In many of these animals, the instinctive equipment of the organism is so closely, so rigidly, adjusted to the normal environment of the species that it is only with great difficulty that their behavior traits can be modified through experience.

Yerkes, R. M.: "The Intelligence of Earthworms," *Journal of Animal Behavior*, 1912, Vol. 2, p. 332.

Turner, C. H.: "Behavior of the Common Roach (*Periplaneta orientalis* L.) in an Open Maze," *Biological Bulletin*, 1913, Vol. 25, p. 348.

Triplett, N. G.: "The Educability of the Perch," *American Journal of Psychology*, 1901, Vol. 12, p. 354.

Yerkes, R. M.: "The Formation of Habits in the Turtle," *Popular Science Monthly*, 1901, Vol. 58, p. 519.

Yerkes, R. M.: "The Instincts, Habits, and Reactions of the Frog: I—Associative Processes of the Green Frog," *Harvard Psychological Studies*, 1903, Vol. 1, p. 579.

Porter, J. P.: "A Preliminary Study of the Psychology of the English Sparrow," *American Journal of Psychology*, 1904, Vol. 15, p. 313.

A summary of what is known concerning the learning ability of different species is given by Washburn, M. F.: *The Animal Mind*, pp. 246 ff. New York: The Macmillan Co., 1926.

This condition is a very efficient one, provided the environment is sufficiently stable so that the organism does not meet new situations to which the instinctive equipment is unadjusted. When such is the case, the organism will be greatly handicapped in its adjustment, even to failing to make the necessary adjustment, with the consequence that death ensues.

The implications of the fact of this rigid adjustment of instinctive equipment to normal environment with reference to the importance of the ability to learn are quite clear. When the environment in which the organism normally lives is a changeable and complex one, survival depends upon the ability of the organism to modify its reaction through experience, and that is learning. This point may be further emphasized by the reminder that there are certain abnormal human beings in whom the ability to learn is low. These are the feeble-minded. For humanitarian reasons, society puts such individuals into institutions where the environment is relatively stable and simplified to their level.

Although, as we have indicated, learning ability can be found throughout the phylogenetic scale, in this chapter we shall deal with learning phenomena as they are manifested primarily in the mammalian series. Some limitations must be fixed, and it is the mammals that have received the most attention, from the experimental standpoint, in recent years.

Typical Methods of Studying Animal Learning

It happens that scientists of three different nations have contributed three rather characteristically different methods for the study of learning in animals. These three nations are Russia, Germany and America.

The Russian scientist is Pavlov, and his method for the study of learning, as well as many other phenomena, is

known as the conditioned reflex method. We need not discuss this procedure, as it has been described and many of the results given by Doctor Liddell in the preceding chapter.

Of the American methods, the two that are the most used are: (1) the problem box method, which was first used under controlled experimental conditions by Thorndike,⁽³²⁾ and (2) the maze method, contributed by Small.⁽²⁶⁾ Other methods that have been used by Americans are the multiple choice technique, which was first used in principle by Hamilton⁽¹¹⁾ and later was developed by Yerkes.⁽⁴²⁾ In addition to these methods, there are various kinds of apparatus for the study of the ability of the animal to learn discriminations (see Chapter VII).

The maze is, essentially, a tortuous pathway, usually with some byways leading from it ending blindly (the blind alleys or *cul-de-sac*). It is particularly adapted to the use of the rat as the subject of the experiment, although it has been used with many other species, including the human being. However, since the rat is easily maintained in good health, multiplies rapidly, is active and alert, and is economical to feed, it is used a great deal by experimenters in the field of animal psychology. Therefore, we find many experiments on learning done with the rat as the subject and the maze as the problem. Figure 47 shows the ground plan of a modified Carr maze. The number of patterns of pathways that may be used for a maze is, of course, practically without limit. However, certain patterns give better results than others.*

The problem box is a box or cage with a door fitted in it. This door is held shut by some kind of a latch or hook. In some experiments, the animal is placed inside the box, his task being to learn how to get the door open in order to

* A comparison of many different patterns of mazes will be found in: Warner, L. H., and Warden, C. J.: "The Development of a Standard Animal Maze," *Archives of Psychology*, 1927, No. 93, pp. 1-35.

get out and secure his food—which is usually used as the incentive. This was the procedure employed by Thorndike,⁽³²⁾ who used cats as the subjects, in his early work. In

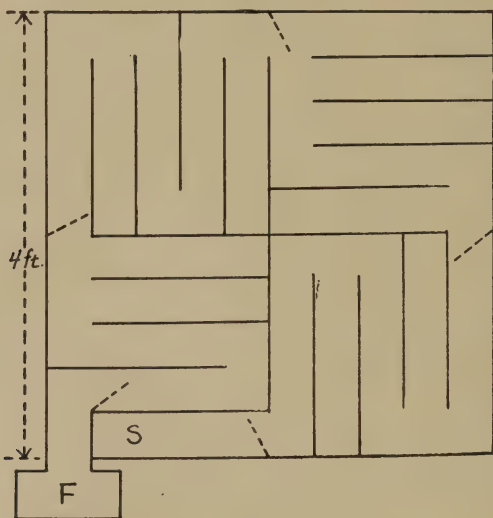


Fig. 47.—Modified Carr maze. *F* indicates the food box; and the animal is inserted at *S*. The dotted lines indicate doors that are operated by the experimenter to prevent the rat's retracing much of his progress. The pattern of this maze may be changed by sliding the partitions to other positions. The pattern shown was used by C. P. Stone ("The Reliability of Rat Learning Scores Obtained from a Modified Carr Maze," *Journal of Genetic Psychology*, 1928, Vol. 35, pp. 507-521).

other experiments, the animal is placed outside of the box and the incentive on the inside. In Figure 48 is shown a perspective drawing of an inclined-plane box of the type in which the incentive is placed on the inside.*

The problem box has never been as widely used as the maze, probably because an error is not as easily defined and

* Photographs of the problem boxes used by Thorndike will be found in: Adams, D. K.: "Experimental Studies of Adaptive Behavior in Cats," *Comparative Psychology Monographs*, 1929, Vol. 6, No. 27.

recorded in this type of problem as in the maze. It is, however, a very useful technique for some species, for example, monkeys and apes, which are not particularly adapted to the maze situation.

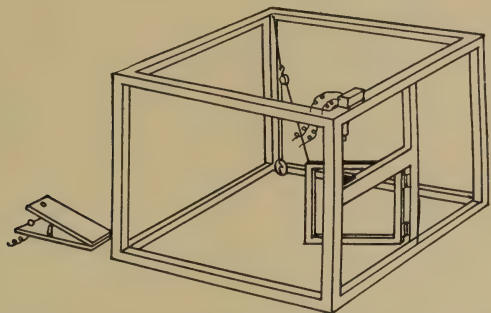


Fig. 48.—An inclined-plane problem box. By stepping on the inclined plane to the left, the rat causes an electrical contact that allows the door to open. Only the frame of the box is shown; in actual use it is covered by wire mesh. (Adapted from Watson,⁴⁰ page 97, after Basset.)

The maze and problem box techniques are particularly adapted to experimentation upon what is called “trial-and-error” learning. In order to illustrate what is meant by this type of learning, we cannot do better than to quote from Thorndike’s description of the behavior of his cats in the problem boxes.

The behavior of all but 11 and 13 was practically the same. When put into the box, the cat would show evident signs of discomfort and of an impulse to escape from confinement. It tries to squeeze through any opening; it claws and bites at the bars or wire; it thrusts its paws out through any opening and claws at everything it reaches; it continues its efforts when it strikes anything loose and shaky; it may claw at things within the box. It does not pay very much attention to the food outside, but seems simply to strive instinctively to escape from confinement. The vigor with which it struggles is extraordinary. For eight or ten minutes, it will claw and bite and squeeze incessantly. With 13, an old cat, and 11, an uncommonly sluggish cat, the behavior was different. They did not struggle vigorously or continually. On

some occasions, they did not even struggle at all. It was therefore necessary to let them out of some boxes a few times, feeding them each time. After they thus associate climbing out of the box with getting food, they will try to get out whenever put in. They do not, even then, struggle so vigorously or get so excited as the rest. In either case, whether the impulse to struggle be due to an instinctive reaction to confinement or to an association, it is likely to succeed in letting the cat out of the box. The cat that is clawing all over the box in her impulsive struggle will probably claw the string or loop or button so as to open the door. And gradually all the other non-successful impulses will be stamped out and the particular impulse leading to the successful act will be stamped in by the resulting pleasure, until, after many trials, the cat will, when put in the box, immediately claw the button or loop in a definite way.*

Because the maze and problem box techniques do emphasize the trial-and-error learning to the exclusion of other possibly more intelligent types of behaviors, Köhler, the German psychologist, has criticized them. In his investigations, chiefly upon apes, he has used what he calls the "roundabout" procedure. In using this procedure, the problems to be learned are so arranged that the animal can survey the total situation.

In this connection, Köhler ⁽¹⁷⁾ writes,

American animal psychology makes animals (or people) seek the way out of mazes, over the whole of which there is no general survey from any point inside; the first time they get out is, therefore, necessarily a matter of chance, and so, for these scientists, the chief question is how the experience gained in such circumstances can be applied in further tests. In intelligence tests of the nature of our roundabout-way experiments, everything depends upon the situation being surveyable by the subject from the outset.

Köhler likewise objects to Thorndike's use of problem boxes. He writes a criticism in the following strain:

* Adams ⁽¹⁾ has repeated Thorndike's experiment and maintains that this paragraph does not give a typical picture of the cats' behavior if they are accustomed to the experimental situation. Nevertheless, this paragraph is classical as a description of trial and error.

It is somewhat astonishing to find that [in Thorndike's experiments] cats and dogs were frequently placed in cages containing the extreme end only of one or the other mechanism, or allowing a view of ropes or other parts of the mechanism, but from which a survey over the *whole* arrangement was not possible.

As the result of the use of the roundabout methods, Köhler has emphasized what he terms *learning by insight* as opposed to trial-and-error learning. We shall discuss this phenomenon in more detail in the succeeding chapter.*

It should be noted, however, that the methods and findings of the German psychologists (Köhler and others) who belong to the Gestalt school have greatly influenced many psychologists in America. The student need only study Tolman's ⁽³³⁾ or Wheeler's ⁽⁴¹⁾ recent book to have brought forcibly to his mind an example of this influence.

There remains to be mentioned in more detail the multiple choice technique. The essential part of the apparatus is a series of similar compartments. These compartments are not all used at any one trial, but they are used in groups of a given number: let us say, for example, groups of three. At one trial, the three compartments on the right end of the series of ten are open; at another trial, those on the left end; at another, those in the middle; and so on. Of the group of three open compartments, only one contains food. This one, however, in any particular experiment, always bears the same spatial relationship to the open compartments. For example, the food-bearing com-

* It does not lessen our appreciation of the great significance of the contributions of Pavlov, Thorndike, and Köhler to remember that the procedure that each stresses is not original with him. The process of conditioning has been known as long as we have known the law of contiguity; problem boxes in one form or another have been known for ages; the principle of the maze goes back to Greek mythology; and the roundabout procedures were used by Hobhouse.⁽¹³⁾

The contributions of the men in question lie in their adaptation of these principles to exact experimental control, and in the fact that they have used these methods in attacking problems of great significance.

partment may always be the left one in the group of three. In this case, therefore, the problem for the animal is to learn always to go to the left compartment of the group of three open compartments, no matter where that group may be located in the total series.

It is obvious that the behavior of the animal in this problem must necessarily be of the trial-and-error sort, at least in the beginning, because there is no "insightful" way in which it can determine the compartment containing the food. Later, of course, it may suddenly grasp the system that the experimenter is using and after that make few, if any, errors.

Up to this point, we have discussed general methods that are used for the study of learning in animals. It goes almost without saying that there are many modifications of these methods for particular purposes. Later in the chapter, when we discuss individual experiments, we will indicate the modifications used in each experiment.

The Learning Curve

In our study of learning, we find it convenient to represent the progress of learning by graphical means. In the study of learning by the American methods, particularly, the rate at which the animal modifies his reactions is usually represented by the rate at which he eliminates errors or time in succeeding trials with the apparatus. The tendency in recent years has been to place greatest reliance upon error records, especially in the maze problem.

The rate of elimination of errors is most conveniently shown by plotting a learning curve. In Figure 49 is shown a learning curve based upon the total error record per trial of a group of 103 rats which were given one trial in running a maze per day for twenty-five days. It is seen that there is a relatively rapid descent of the curve in the first few trials, and that the rate of descent of the curve gradually

decreases with progressive trials. It is because of this fact that this type of curve is called a *negatively accelerated curve*.* This is the usual form that the learning curve takes under standard experimental conditions. It is characteristic of much of human as well as animal learning.

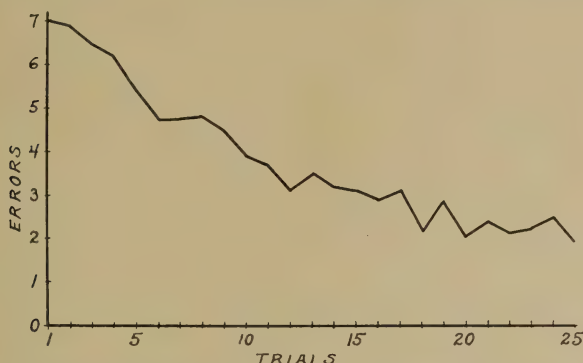


Fig. 49.—Learning curve of a group of rats on a multiple-T type of maze. If a sufficient number of trials were given, the curve would continue its downward course until it reached the base line.

If, however, some factor that affects the course of learning is varied, there will be a change in the rate of descent of the curve as compared with that of the curve obtained under constant experimental conditions.

If we then plot the two curves, using the same ordinate and abscissa, we will have a graphic representation that shows the effect of changing the experimental conditions. A number of situations of this nature will be discussed later.

The Relation of Learning to Certain Variable Factors

We are now ready for a discussion of some of the experiments to determine the factors or conditions that affect

* If correct responses are plotted on the ordinate, the curve will ascend rather than descend. It is still, however, a negatively accelerated curve.

learning. It will be impossible to discuss all the factors of this nature that have been investigated.* Only a few will be chosen, to give the reader a slight notion of what has been done and what the possibilities are.

Motives and incentives.—One of the problems of great general importance and especial importance in its relation to learning is the problem of motivation and incentive. We will not discuss this problem in its general aspects, as that has already been done by Professor Stone, in Chapter IV. However, we do wish to give some attention to the problem in its relation to learning.

One of the first questions that come to mind is: Will the animal learn a problem when the motive or internal drive is present but the incentive that satisfies that drive is lacking?

Blodgett⁽³⁾ and Tolman and Honzik,⁽³⁴⁾ among others, have investigated this question, using rats as subjects. The general procedure in Blodgett's experiment was to allow hungry rats (that is, hunger was the drive or motive) to explore a maze, but without food (the incentive) at the exit of the maze. He used three groups of animals. Group I (containing 36 rats) ran the maze once a day for seven days. They were "allowed to eat for *three minutes in the food box at the end of each run.*" Group II (containing 36 rats), litter mates of Group I, were treated the same as Group I save that they found no food in the food box *for the first six days.* Each rat was kept in the food box for two minutes and one hour later was fed in another cage. On the seventh day and the two subsequent days, they were treated exactly as Group I was treated. Group III (containing 25 rats) were treated as were Group II except that

* A comprehensive bibliography of reference bearing on this question and others in the field of learning and memory from the standpoint of experimentation upon human subjects has been compiled by McGeoch, J. A.: "The Psychology of Human Learning: A Bibliography," *Psychological Bulletin*, 1933, Vol. 30, pp. 1-62.

food was introduced on the third day rather than the seventh.*

Figure 50 shows the error curves for these three groups. It is quite obvious that little or no learning takes place objectively as long as the incentive is not given at the completion of the run. However, some learning is progressing,

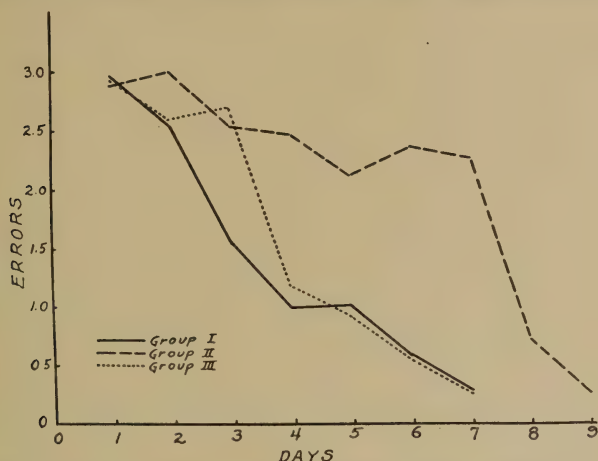


Fig. 50.—Learning Curves of Blodgett's Three Groups of Rats. (See text.)

as is evidenced by the very great drop in the curves for Groups II and III on the day following the day on which they first found food in the food box. This learning has been termed by Blodgett *latent learning*.

The point that we want to emphasize at the moment, however, is that there is little objective evidence of learning as long as the incentive or reward is lacking.

The experiment by Tolman and Honzik⁽³⁴⁾ is essentially the same as that of Blodgett. These two experimenters used a longer maze than the latter's, but it embodied the same multiple-T principle (see Chapter XIII). They used

* It should be understood that in all learning experiments, unless otherwise mentioned, each animal is introduced singly into the apparatus.

three groups of animals, which were designated as follows: HNR, that is, hungry but at no time receiving food at end of maze; HR, that is, hungry and receiving food at the end of each trial; and HNR-R, that is, hungry but receiving no food at the exit of the maze until the end of the eleventh trial. In Figure 51 are shown the learning curves for these

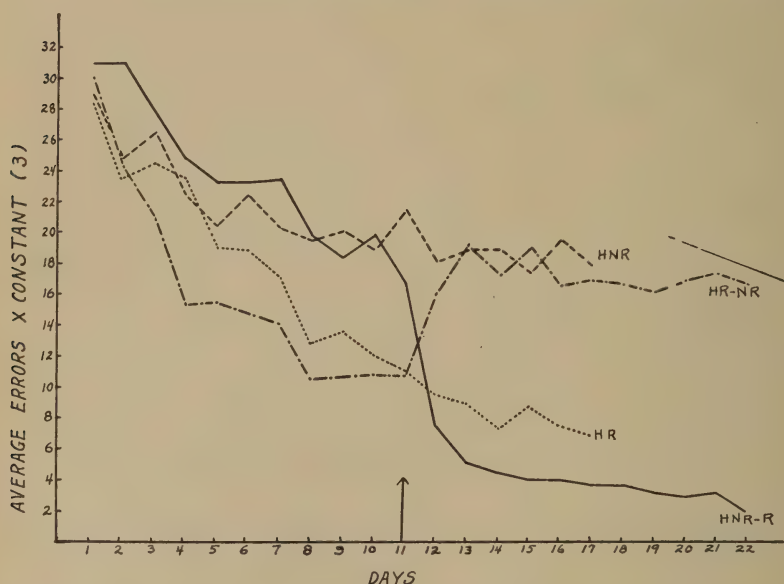


Fig. 51.—Learning Curves of the Groups of Rats Run by Tolman and Honzik. (See text.)

three groups. Again we see that the group that was not rewarded (HNR) did not show much improvement in terms of the elimination of errors. The group that was rewarded (HR) shows the usual gradual but progressive elimination of errors. Now note especially the curve for the HNR-R group. There is very little improvement until the twelfth day, at which time there is a relatively large decrease in the number of errors made. This again indicates "latent

learning," and also demonstrates that, in order for this "latent learning" to be manifest, the proper incentives must be introduced into the situation.

It remains to be added that in both of the experiments cited above, the time curves indicate the same conclusions that we have stated on the basis of the error curves only

We have implied above that the incentive must be appropriate to the motive in order to obtain maximum benefits in terms of objective indications of learning. Experimental results bearing directly upon this point were secured by Elliott.^{(8)*} His error learning curves for three groups of rats are reproduced in Figure 52. The respects in which the groups differed are indicated in the figure. Note particularly the curve for Group *F*. This group was only slightly thirsty, and when the reward was changed to water on the tenth day and thereafter, there was a marked increase in number of errors made, beginning with the eleventh day. This means that the incentive has become less appropriate with reference to the drive, with the consequence that there is a detrimental effect upon the progress of learning. Knowing this, we of course may infer that the complete removal of an effective incentive during the course of learning would have the maximum detrimental effect. An experimental proof of this inference is to be found in the Tolman and Honzik experiment. Refer again to Figure 51, and notice the curve for the group labelled HR-NR (hungry reward—no reward). This group was hungry at each introduction to the maze throughout the experiment, and for the first ten days they received food, the appropriate incentive. However, beginning with the eleventh day and thereafter, they did not receive the food until two hours later. As the curve shows, this had a markedly detrimental effect in that there was a large increase in the number of errors made.

* The same experiment is reported in greater detail in Chapter IV, p. 101 ff.

Experimentation (by Szymanski ⁽²⁹⁾) has also shown that the converse (change of drive with a constant incentive) will produce the same result, that is, degeneration of the

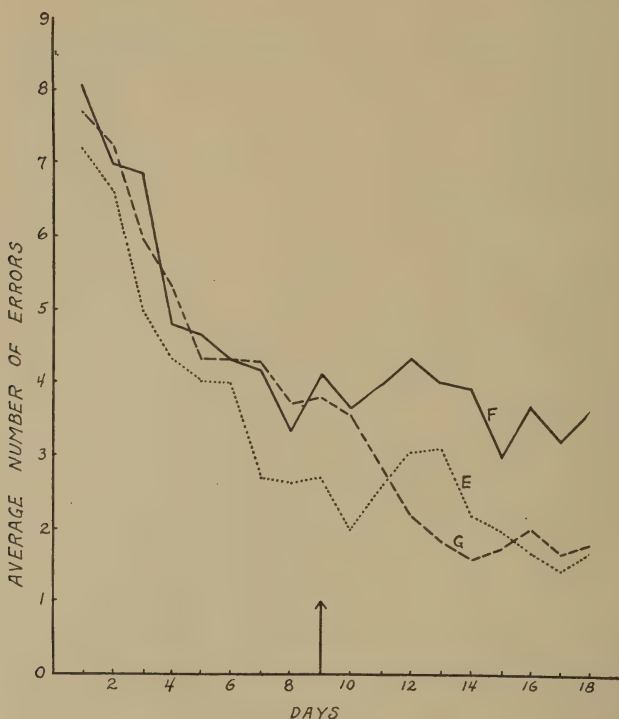


Fig. 52.—Learning curves of the groups of rats run by Elliott. Group E was very hungry and very thirsty; Group G was slightly hungry and very thirsty. All groups were rewarded with food for 9 days and then given water reward.

maze habit, and that a given drive and its appropriate incentive may be changed to another drive with its appropriate incentive without any detrimental effect upon learning except during the trial in which the change of drive is made. ⁽⁹⁾

Another problem of great interest is concerned with the effect of delaying the giving of the incentive after the animal has completed the performance. It is generally assumed that the animal should have immediate access to the incentive as soon as he has completed the trial of the problem. Certain theoretical considerations would lead one to expect this to be the case. In view of this situation, it is rather peculiar that we do not have an extended systematic attack upon this problem.

Warden and Haas ⁽³⁹⁾ have recently studied the problem, using three groups of rats: (1) a control group that was fed immediately at the end of each trial; (2) a group that was fed one minute after the completion of each trial; and (3) a group that was fed five minutes after the completion of each trial. The results show no appreciable difference in speed of learning the maze in the five-minute group and the control group. The one-minute group, however, learned somewhat more slowly than the control group, although the difference is not statistically significant.

The results of this experiment are probably vitiated by the fact that, although the animals in the one- and five-minute groups could not eat their food until after those intervals of time had elapsed, nevertheless the food was in the food box and they had the opportunity to smell it. Bruce ⁽⁴⁾ conducted an experiment in which he ran rats in a maze on ten successive days, allowing them to eat immediately in the food box after each trial. On the eleventh day and thereafter, the food was in the box but was covered by wire mesh so that the animals could not eat it. The results of this experiment lead him to make the statement, "It would appear that the pre-current responses involved in seeing and smelling are enough of a surrogate for the consummatory response of eating to keep behavior oriented toward the food box."

Thus, we see that the experiment on delayed incentive

should be done with the incentive entirely removed, so that the animal can have no contact with it whatsoever.

Another problem of great importance is concerned with the relative value of so-called "negative" and "positive" incentives. The latter is something to which the animal reacts positively, such, for example, as some food. The former is something to which the animal reacts negatively, that is, punishment in some form, such, for example, as an electric shock. Parents, in dealing with children, and society, in dealing with criminals, tend to make a rather large use of "negative" incentives. Both parents and society are somewhat inclined to overlook the possibility that "positive" incentives may also have value.

Psychologists have attacked this problem with both animal and human (see, for example, the work by Hurlock⁽¹⁵⁾) subjects. This is by no means a simple problem, as there are many factors that must be taken into consideration. Perhaps one of the most important of these factors is the degree of difficulty of the task that is presented to the subject for solution.

One of the more recent experiments in connection with the problem was done by Warden and Aylesworth.⁽³⁷⁾ The task to be learned by their rats was a relatively easy brightness discrimination problem (see Chapter VII). They used three groups of animals: (1) a reward group, to which food was given when a correct response was made, but which, if an incorrect response was made, were simply removed from the apparatus until the next trial; (2) a punishment group, to which punishment (electric shock) was given when they made an incorrect response, and which were removed from the apparatus when they made correct responses; and (3) a reward-punishment group, which were given food for a correct response and punishment for an incorrect response.

Figure 53 shows the learning curves for these three groups. It is quite evident that learning occurs most rap-

idly under the reward-punishment conditions, and that reward alone gives the poorest results. Although there are several experiments on this general question, it is recognized that the problem must be reworked in a more systematic manner under a number of different conditions before any very specific conclusions may be definitely stated.

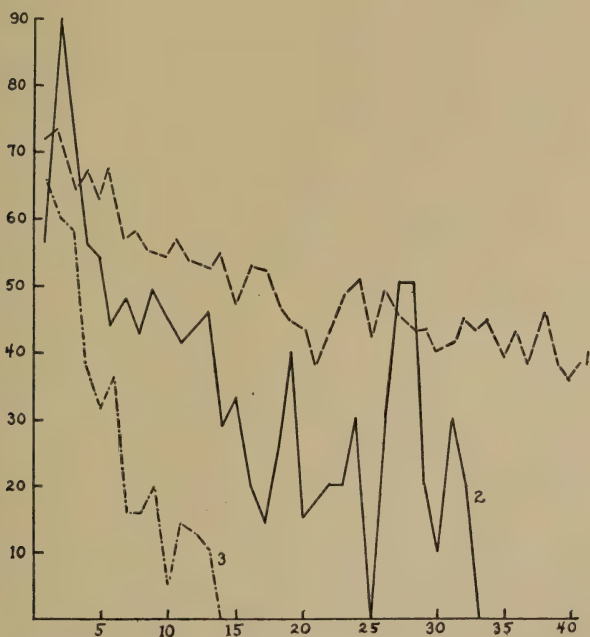


Fig. 53.—Learning curves of the groups of rats used by Warden and Aylesworth. Curve 1 is for the reward group; Curve 2, the punishment group; Curve 3, the reward-punishment group.

We wish to mention one more problem in this general field of the relation of motives and incentives to learning. The assumption is, we believe, generally made that a child should be punished immediately after he has committed an infraction of the rules of behavior. This assumption, how-

ever, is not always acted upon. When Johnny makes a misstep, mother sometimes says, "I'll tell your father when he gets home, and he will attend to you." Johnny may or may not take this statement seriously, depending upon his previous experience with similar situations. However, the question remains: Would it not be more effective, if punishment is to be given at all, to give it immediately?

Data with reference to this question can be obtained upon animals relatively easily.

Warden and Diamond ⁽³⁸⁾ have carried out experiments relative to this question, using a very simple problem with rats. Their results are given in Table XII.

TABLE XII
TRIAL-AND-ERROR SCORES IN LEARNING A LEFT TURN WITH
DELAYED PUNISHMENT

<i>Length of Delay</i>	<i>Total Score</i>	
	<i>Trials</i>	<i>Errors</i>
0 seconds	37.8	34.5
4 seconds	81.0	68.0
8 seconds	71.5	66.5
12 seconds	83.5	75.0
20 seconds	108.0	101.0

From these data, it appears that there is a general tendency for the effectiveness of punishment to decrease with an increase in the length of the interval elapsing between the time of making the error and the giving of the punishment.

Tuitional controls in learning.—A part of educational effort is expended in the endeavor to teach the human subject the solutions to problems. We believe that it is more economical to teach the solutions than it is to let the subject arrive at the solutions without guidance and at the expense of a great deal of time and effort used in the making of errors. In other words, we attempt in many cases to prevent the learner from making many, if not all, errors. It would seem reasonable that this procedure should prove

beneficial. Carr ⁽⁵⁾ has pointed out, however, that there are many questions involved in this process that should be investigated from an experimental standpoint. Some of these questions, as he states them, are:

Can a subject, either an animal or a human subject, master a problem more quickly when his reactions to that problem are guided and directed by the experimenter than he can when he is compelled to solve that problem on his own initiative? What is the relative value of the various methods and devices of aiding the subject that may be employed? Are animals and human subjects equally susceptible to any given method of tuition? Can you give a subject too much help? In what part of the learning process should this guidance be introduced in order to secure the best results? Granted that an individual can solve a problem more quickly when aided, will not an individual who solves that problem on his own initiative master it more effectively, that is, will he not retain it for a longer time, and will he not be able to utilize the skill and knowledge obtained more effectively in dealing with other similar problems?

Many different experiments have been done along these lines, some using animals and some using human subjects. Carr ⁽⁵⁾ has summarized many of these experiments, and from his summary we take Table XIII, based upon the results obtained by Koch ⁽¹⁶⁾ with white rats in the maze problem.

The form of guidance used was to block the blind alleys in the maze for a given number of trials, so that during these trials the animals were forced to take the correct path without making errors. The trials in which guidance was given were inserted in different positions in the course of learning for various experimental groups. The control group received no guided trials at all.

The table indicates the number of unguided or undirected trials (derived from the control group) equivalent to one guided trial when the guided trials are placed in different stages of the learning process as indicated by the numbers in parentheses.

TABLE XIII

THE INFLUENCE OF MECHANICAL GUIDANCE WITH WHITE RATS

<i>Number of Guided Trials</i>	<i>Number of Undirected Trials That Are Equivalent to One Guided Trial</i>			
2	4.2 (1-2)	2.5 (6-7)	1.0 (11-12)	
4	3.0 (1-4)	1.4 (5-8)	1.2 (9-12)	1.2 (13-16)
6	3.0 (1-6)	2.6 (4-9)	.7 (7-12)	
8	1.7 (1-8)	.4 (3-10)	.9 (5-12)	
12	.8 (1-12)			

This table shows that guidance is effective in mastery of the problem. If, in any case, it had not been, the value not in parenthesis would be negative. In some cases, however, the guided trials are less effective than an equal number of unguided trials, as indicated by the fact that some of the values are less than one. There are several other conclusions that may be drawn from this table. The reader will find it of interest to formulate these conclusions himself.

As a general rule, in animal learning, a limited amount of guidance is effective, although this limit may be easily exceeded. There are also a large number of other factors that help to determine the effectiveness of guidance. For a consideration of these, the reader must go to the original literature.

Age.—In recent years, a good deal of emphasis has been placed upon adult education. The question that naturally arises immediately is whether the adult learns more effectively or less effectively than the young person. There is an old adage that states that “you cannot teach an old dog new tricks.” Is this correct, or, to state the matter in general terms, “What is the relationship between learning ability and age?”

Thorndike ⁽³¹⁾ has recently treated this question extensively from the standpoint of the human subject. However, in the case of the human being, the picture is complicated by many factors that are not altogether easy to control. Consequently, it is important to attack the problem with animal subjects. This has been done to the best advantage by Stone ^(27, 28) with the use of our old friend, the rat, as subject. He summarizes his results in the following quotation:

For practical purposes, it now seems sufficiently exact to say that *in the absence of interfering habits, approximately maximum learning rate for mazes, problem boxes, simple light discrimination, and other novel situations thought to be of similar or equivalent nature is attained by young albino rats of 30 to 75 days. The majority of my experiments suggest that it is attained at an age nearer 30 than 75 days. The level of maximum learning rate in all probability does not decline in normal animals having no interference habits throughout the first two-thirds or more of their life span, i.e., during the first two years of life. Should subsequent experiments reveal a slight superiority for either the young, the adult, or the early senescent group, there will, nevertheless, be found a very great amount of overlapping of ability between the respective groups.*

Donaldson ⁽⁷⁾ indicates that the average life span of the rat, under good environmental conditions, is about three years. On the basis of the development of the rat as compared with that of the human being, the former at three years of age corresponds to a man of ninety years. Therefore, a rat two years of age, the maximum age used by Stone, would correspond to a man of sixty. It is, of course, unscientific to assume that comparisons of this sort are necessarily valid. However, it is interesting to do so, and, in view of the fact that experimentation with the human being on this problem as well as many others is subject to so many uncontrollable factors, the comparison is not altogether unjustified.

A problem that intrigues the writer in connection with

age and learning ability is whether or not age has any differential effect upon different degrees of ability. This problem could best be solved with the use of selected groups that differ markedly in ability. The way will be open for attack upon this question when strains of good and poor maze learners are well isolated. Attempts to isolate such genetically different strains are now being made in the laboratories of the University of California and the University of Minnesota (see Chapter XIII).

Another problem of interest is whether or not there is any difference in the average span of life of groups of individuals differing in learning ability. It might be assumed that among human beings the better learners would be subject by virtue of that fact to greater stresses and strains in life that might tend to shorten the life span. Or, conversely, they may be able to adapt so much more efficiently than the poorer learners that the effect is just opposite. It may be also that, in general, greater learning ability is accompanied by a more robust physical constitution. Terman's ⁽³⁰⁾ study of gifted children indicates that this may be the case, so far as the human being is concerned. This advantage may make for a longer span of life. For the most part, however, these problems still await solution.

Dietary deficiencies.—There are always those in the human population who, for one reason or another, do not eat proper food. The numbers of these individuals may increase greatly as the result of the occurrence of widespread economic upheavals, wars, or natural disturbances.

An organism may suffer one or the other or both of two kinds of dietary deficiencies. That is, it may receive a diet containing all the necessary elements for the satisfactory maintenance of life, but it may not receive a sufficient amount of this diet. This is a quantitative deficiency. On the other hand, the organism may receive a sufficient bulk of food material, but this food may lack or be deficient in

one or more necessary elements. This is a qualitative deficiency.

Paterson ⁽²³⁾ summarizes the evidence with reference to the relation of malnutrition to intelligence in human subjects. He concludes that at present there is no demonstrable relationship between undernourishment and intelligence. It is obvious, however, that there are many important points that are given little attention by experimenters in dealing with this question from the standpoint of human subjects. For example, is the malnutrition due to a qualitative or a quantitative dietary deficiency? Also, there may be no dietary deficiency at all, but the apparent malnutrition may be caused by the malfunctioning of some organ of the body.

It is much easier to control these factors and many others if animal subjects are used. Therefore, the general problem of dietary deficiency in relation to learning has been attacked by several investigators with animals. Of all of these, Maurer and Tsai ⁽²¹⁾ have reported the largest differences. They subjected nursing rats to a depletion of the vitamin B complex, but after the nursing period they fed them a normal diet. At the age of seventy days, these rats showed very much poorer maze learning records than normal animals.

Fritz ⁽¹⁰⁾ also investigated the effect of vitamin B deficiency upon learning. However, his animals were from ninety to one hundred days old before the deficiency was introduced. He finds that this deficiency decreases the speed with which the animals traverse the maze, but that their accuracy as compared with that of a normal group is not affected.

Anderson and Smith ⁽²⁾ investigated both quantitative and qualitative deficiency with rat subjects. The animals subjected to the deficiencies made somewhat better learning records than the normal groups. Upon realimentation, the

records of the stunted animals and those of the normal animals tended toward similarity.

In work upon dietary deficiency, it is difficult to know whether the difference in learning between the normal animals and the group subjected to the deficiency is owing to an effect upon the learning ability of the animals or to a change in motivation. The influence of motivation upon learning we have already discussed, and we do not need to repeat it here. However, it is quite possible that a dietary deficiency should have an effect upon motivation that would be reflected in the learning record. This is particularly possible if the motive that is used is hunger.

Ruch ⁽²⁴⁾ has attempted to obviate this ambiguity in the interpretation of results by using a water maze. This is a maze that is filled with water to such a depth that the rats must swim through it. The motive is not hunger, but the tendency of the animal to escape from water.

In this maze, he used several groups of quantitatively stunted animals and also animals that were given all the food that they would eat. He finds that the stunted animals learn this maze more quickly than the control group. We are still left somewhat in doubt, however, as to whether this difference may not be interpreted in terms of motivation. Stunted animals are hungry animals, and hungry animals, within limits, are more active than satiated animals. It is possible that heightened activity would lead more quickly to escape from the water maze. We see, therefore, that it is not at all easy to be able to say that a dietary deficiency does or does not affect learning ability as such.

There is great opportunity for further work upon this problem. Nutritional laboratories are daily discovering new facts about food elements that affect the physical well-being of the individual, but the surface has only been scratched in this respect with reference to psychological abilities.

Other factors in relation to learning.—It is impossible, because of space limitations, to discuss all the factors that have been investigated in relation to learning. We have discussed four such factors in some detail. A discussion of some others will be found in other chapters. We will content ourselves with giving a partial list in order to indicate to the reader the problems that have been attacked.

Experiments have been done upon the following problems: (1) distribution of practice; (2) whole versus part learning; (3) length of material to be learned; (4) emotional disturbances; (5) sex; (6) drugs (see Chapter V); (7) ligation of arteries supplying the brain; (8) temperature; (9) oestrous cycle; (10) endocrine glands (see Chapter V); (11) surgical interference with the nervous system (see Chapter VIII); (12) positive and negative transfer; and (13) retroactive inhibition.

The final word has been said with reference to few, if any, of these problems. The simplest is exceedingly complex. Each must be considered in relation to many of the others. A long stream of arduous and intricate research must still flow beneath the bridge before we can feel relatively confident that satisfactory answers have been found.

Cues Used in Learning

It is interesting to note that, in spite of all the work that has been done on learning, experimenters are not sure just what sense organ functions in the learning of certain problems. Of course, in problems on sensory discrimination (see Chapter VII), the animal is forced to use a certain sense organ, if the experiment is well controlled. Also, in the case of Köhler's roundabout problems, vision seems to be a very important sensory field.

However, in the maze and problem box problems, the situation is not so clear. So far as the rat in the maze is concerned, Watson thought he had largely solved the prob-

lem. By a process of eliminating sensory fields, he came to the conclusion that the rat must learn the maze by the use of the muscle sense (kinæsthesia). He found that the animal could run the maze when one after another of his sense organs had been eliminated. Watson, however, knew of no method of eliminating the muscle sense, so that he could give no positive proof of his contention by the process of elimination. However, in a special maze,⁽⁴⁰⁾ in which the alleys could be shortened or lengthened, he believes that he has positive proof. If, after an animal has learned the maze, the alleys are shortened, the animal, according to Watson, will run into the walls; or if the alleys are lengthened, it will try to turn before the end of the alley. These and other data cause him to make the statement: "We seem forced to conclude that in the rat, kinæsthetic arcs are the only ones necessary at any stage of the formation of this habit." He therefore resolves the "maze habit process into the functioning of a serially chained kinæsthetic arc system."

This particular doctrine has received widespread attention and has been applied to many human habits of everyday life. It has also initiated a large amount of research, most of which we cannot discuss here. The result of this research has been, however, to question the conclusion that the maze habit is simply a concatenation of kinæsthetic arcs.

Watson⁽⁴⁰⁾ himself realized that the situation might not be as simple as he had described it. For example, he states that the animals are confused by the rotation of the maze 180 degrees. This, of course, should not occur if kinæsthetic arcs are all that operate, inasmuch as the units in the maze still bear the same relationship to each other.

Hunter,⁽¹⁴⁾ in order to test what the animal can accomplish with kinæsthesia, designed the temporal maze that is diagrammed in Figure 54.

In this maze, when the rat is forced to go two times to

the right and then two times to the left (that is, RRLL), he fails to learn the problem. In this situation, there are no differential cues for the second right turn and the second left turn unless the animal can derive such cues from his kinæsthetic impulses. Apparently, the rat is not able to do this.*

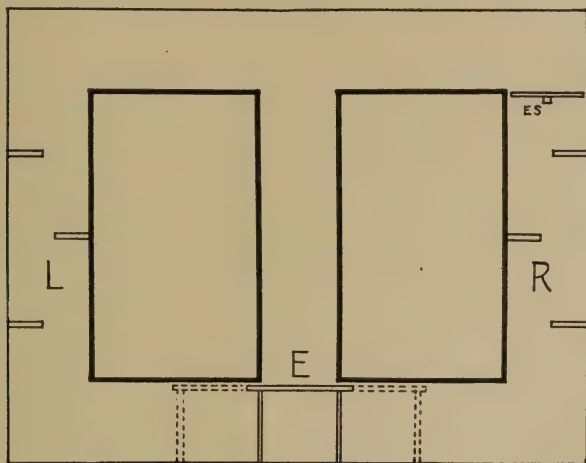


Fig. 54.—The temporal maze. A stop, *ES*, may be inserted into either alley, *R* or *L*, to prevent the animal from completing a tour on the wrong side. The animal is inserted into the apparatus at *E*. The stop just below *E* may be shifted into the positions indicated by the dotted lines in order to force the animal into the central alley again after the completion of each tour. (After Hunter.)

This, of course, does not prove that kinæsthesia is not used in maze learning, but it does show us one of the limitations of this sensory field.

Another attack upon this general problem was made by MacFarlane,⁽²⁰⁾ who taught rats a maze in the usual fashion,

* This problem of double alternation will be discussed in another connection in Chapter XI.

and then filled the maze with water in such a way that instead of running, the animals had to swim.

He found that this change caused very little disturbance in error score. The same procedure in the reverse order was also used, with the same result. He maintains that the change from running to swimming, or vice versa, must have been a change in the kinæsthetic pattern, and that, therefore, if kinæsthesia was effective in guiding the animal, there should have been a disturbance.

Lashley and Ball ⁽¹⁹⁾ attempted to eliminate, by double hemisections of the cord in the cervical region, most of the proprioceptive impulses in rats that had learned a maze. They then retested these animals in the maze and found almost perfect retention. They believe that they eliminated or controlled all exteroceptive cues. They conclude that the best explanation of their results is that the maze habit is controlled by some sort of central mechanism that will function independently of sensory cues.

It would be interesting to know whether rats under the conditions of the Lashley and Ball experiment could learn the maze. For, even if we grant that the maze habit, after it is learned, is controlled by a central mechanism, still it seems necessary that this engram must be established originally through some sensory pathway or pathways.

These various experiments indicate that the maze habit is far from being as simple as it was formerly conceived to be. To complicate the problem still further, we have evidence that the rat learns, in some way, the general location of the food box with reference to the starting box. This is shown by the fact that if physical obstacles are removed, it will go to the food over a path that it has never taken before and that is, more or less, a straight path from the entrance to the food box. Dashiell, ⁽⁶⁾ who has studied this phenomenon extensively, believes that it must have some sort of intraorganic basis.

This problem is further complicated by what for want

of a better name we call *preferential tendencies*. Thus, Yoshioka ⁽⁴³⁾ and others have found that rats will group themselves into those that tend to go right, and those that tend to go left, at points where the path bifurcates.

There is also the very evident tendency for the rats to take the shortest path to the food, provided there is the possibility of taking several paths and provided all other factors are equal. We may use Kuo's ⁽¹⁸⁾ experiment as an example to demonstrate this phenomenon, although there are many other experiments that could be used as well. Kuo gave his animals the choice of four paths to the food. These paths were differentiated as follows: Path *A* had in it an electric grill that gave the rat a shock when he ran over it; Path *B* had an arrangement whereby the rat could be confined for a given period of time; Path *C* was a long path; and Path *D* was a short path. At the beginning of the experiment, the animals had no basis upon which to differentiate the paths and therefore went through each to the food approximately the same number of times. However, they soon learned to stay out of Path *A*, in which they would receive the shock. Eventually, Paths *B* and *C* were also eliminated and the animals settled down to the use of Path *D*.

Tolman and Sams ⁽³⁵⁾ also have shown that rats in a maze will learn to take the path that involves the least expenditure of time in getting to the food, although the various paths are equal in all other respects. Tolman ⁽³³⁾ suggests that in all probability the animals will also learn to take the path that involves the least expenditure of effort in terms of overcoming resistance, as, for example, going uphill.

Many, if not all, of these factors enter into the maze learning process, and thus we see that it is a much more complicated situation than it may appear at first glance. These complications necessitate a change in Watson's idea of the rôle of kinæsthesia in maze learning. A discussion

of this change would, however, lead us into a consideration of the whole theory of learning. This will be considered by Professor Tolman in Chapter XII.

Retention

A discussion of learning would hardly be complete unless some mention, at least, were made of forgetting, or lack of perfect retention. Learning and forgetting are complementary processes. If one did not retain from one moment to the next, one would learn little. On the other hand, if one had perfect retention, one would not learn in the ordinary sense of that term. To make these statements clearer, consider for a moment the learning of a maze by the rat. If the animal did not retain something of what it had learned in one trial over the period intervening until the next trial was given, obviously, it would not learn the maze. But, on the other hand, suppose that the rat should retain everything from trial to trial; then it would not learn, because it would not effectively eliminate its errors. In other words, learning and forgetting must go hand in hand in order that progress shall be made to the point where the habit functions smoothly and automatically.*

Retention, as it is investigated in the laboratory, usually involves the question of how much is retained over a relatively long period of no practice rather than over the period existing between trials. The percentage savings method is the method usually used to measure the retention. This method may be expressed in the form of the formula:

$$\frac{O. L. - R. L.}{O. L.} \times 100, \text{ in which } O. L. = \text{the number of trials}$$

*It is possible, of course, to prevent an error by remembering that the error should not be made, rather than by forgetting to make it. The former is probably what happens in the beginning of the learning of a new habit. However, as learning progresses, it seems quite likely that we really forget to make the errors. It is then that the organism performs smoothly in the functioning of the habit.

or errors or the time required to learn the problem, and R. L. = the number of trials or errors or the time required to relearn the problem after the period of no practice.

Unfortunately, little systematic work has been done on retention in animals. There are a number of scattered references to the question in reports dealing primarily with other problems. Schneck and Warden ⁽²⁵⁾ have summarized this material.

Perhaps the most systematic investigation has been done by Tsai. ⁽³⁶⁾ He ran seven groups of rats, with twelve in each group, in a Carr-type maze (see Figure 47). These groups were matched on the basis of their original learning. He then used different periods of no practice, which are indicated in Table XIV with the results:

TABLE XIV

Retention interval in days	7	14	21	28	42	56	84
Percentage of savings	95	94	90	86	80	78	60

When those data are plotted, they give practically a linear curve, which is different from the curve of forgetting found under similar conditions for human beings. The human curve is negatively accelerated. However, we will need further work on this problem before we can say definitely that the curve of forgetting for the rat is the same as or different from that for the human being.

McNemar and Stone ⁽²²⁾ also present some data on the retention by rats of the maze habit. Because in most of their groups other learning problems were inserted during the period of no practice, it is not possible to summarize their data at this place. However, their data indicate that the retentiveness of the rat may be to some extent a function of age, and that other learning experience may influence forgetting of the maze habit.

It is quite likely that many, if not all, of the factors that affect the learning will also affect the retention of that which is learned. This is a matter for experimentation to

decide. And a very important matter it is too, because while it is beneficial for the organism to forget some experiences, it is decidedly detrimental to it to forget others. It is only through our ability eventually to gain knowledge of the factors that affect forgetting that we can hope to help the individual to make an adequate adjustment in this respect.

Conclusion

In this chapter we have discussed problems involving, for the most part, trial-and-error behavior. As we have seen, some problems are so arranged that this type of behavior is the only type possible to the organism. However, even in problems that are arranged otherwise, the animal, as a rule, has a very strong tendency to engage in trial and error first. This is frequently true of the human being also. It therefore behooves us to study every factor that we can discover that is related to learning under these conditions.

Our ultimate aim is, of course, to come to a thorough understanding of the learning process in both human beings and the lower animals. In order eventually to accomplish this, it seems to the writer that we have to study the animal from every standpoint. The animal psychologist cannot afford to isolate himself in his laboratory and study the animal from the psychological viewpoint only. He must enlist the coöperation of other scientists and their techniques.

To attempt to understand the learning behavior or any other function of an organism without regard to the mechanism underlying that function is futile.

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CHAPTER XI

Complex Learning Processes

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Introduction

IN the preceding chapter, we described certain experiments in which the animal is required to learn an act of skill by what is ordinarily termed the *trial-and-error* procedure. In this chapter, we shall describe experiments that permit the animal to use a more ingenious mode of attack. In the preceding chapter, we purposely avoided the question of the fundamental nature of the trial-and-error process. In this chapter likewise, we shall as far as possible avoid a discussion of the fundamental nature of the processes that the animal uses in solving the problems that we shall describe. The answers to these questions we leave to Professor Tolman to state in the following chapter.

Insight

In the preceding chapter, we quoted Professor Köhler's criticism of the problems that American animal psychologists set for their animals. The fundamental point of this criticism is that the methods traditionally used by the Americans do not allow the animal to survey the total problematical situation in such a way that it can immediately comprehend the relationships involved, and that, therefore, the animal must rely on the random, largely irrelevant mode of attack upon the problem that is described

by Thorndike in the quotation on page 303. In other words, the animal can only happen by chance upon the solution to the problem. The difficulties that this puts before the animals are vigorously outlined in the form of an analogy by Adams ⁽¹⁾ in the following quotation:

A nearly comparable human situation would be the following: a man is in a small cage. The interior is studded irregularly with buttons—say fifty or a hundred of them. He does *not* know it, but if he presses a certain *four* of them, in any order, a hole, large enough for him to crawl through, will open somewhere in the cage. The correct buttons are so placed that he cannot press any two of them at once. Now suppose he does eventually get out, say by systematically pressing every button. How much will his labor be shortened in his next trial as a result of his success? He may remember which button it was that he pressed last before the door opened, and he may press that at once, but to no effect. He has still to press three, and they may be any of the remainder, and he does not know whether he has to press three more or thirty more. We might arrange in addition that the buttons have to be pushed variable distances, from one to three centimeters, and that some of them should require most of the man's strength to be pushed the required distance. How soon would all the useless pressings disappear?

In order to overcome the difficulties that he believes to be inherent in the traditional American experimentation, Köhler makes use of the "roundabout" method. Experiments of this type are designed in such a manner that the animal can survey the situation and that it has the opportunity to understand, if it is capable of doing so, the relationships that are involved.

The term *insight* has been emphasized by the German school of psychology called the *Gestalt* school, of which Köhler is one of the leading proponents. However, the chief point that it stresses in this connection, namely, that some of the lower animals may react to a relationship if given the opportunity, has been shown, although not emphasized, by experiments that antedate their own. For example, Kinamann ⁽¹¹⁾ showed that monkeys will react to

a relationship between two greys rather than to either of two specific greys.

However, without attempting a specific definition of insight, let us turn our attention to two experiments the results of which indicate this ability. The first of these we will take from Köhler's own work as described in his book, *Mentality of Apes*. The first part of the quotation describes the attempt of Tschego (a chimpanzee) to manufacture a tool, and the last two paragraphs describe the animal's solution of the problem by insight.

Tschego had used sticks as implements during the preceding days and even on the morning before the experiment to be described. A tree is placed about two metres away from the bars, and Tschego is then let into the room. She does not see the tree at first, but when her eye lights on the objective, goes as usual into her bedroom, fetches her blanket, stuffs it through the bars, throws it onto the objective, and tries thus to draw it towards her. For the blanket can be used in two ways, either of which might succeed: beating the goal towards her, or pulling it towards her, after the cover has been thrown over it. The cover is taken away from her; she seizes the tree and makes a great effort to squeeze it, just as it is, through the bars. When that does not succeed, she takes a bundle of straw in her hand, stretches out with it like a stick, and endeavours to pull the objective towards her. As the bundle proves to be too soft and does not drag the objective with it when pulled along, she takes hold of the straw in the middle with her teeth and at one end with her hand, and bends one half over the other, so that a bundle half as long, but incomparably firmer, a real sort of stick, is formed; this she uses at once, and, while it remains long enough, again and again, with complete success. The whole proceeding, from the taking of the bundle of straw which is too soft, up to the use of the firmer one, is one cohering action; it lasts but a few seconds. In this way a method of making implements has been invented that is different from the one expected; Tschego did not, at any time, show any indication of breaking off a branch of the tree, but she clearly showed that she "had present" the use of the stick all through the experiment. The tree, by the way, was only a very small one, which Tschego could easily manage as a whole. This explains why she wanted to use this whole as a stick; but the rough procedure by which she pushes it towards the bars, as if she could thus get it through, is, of course, not justified by the size of the little tree.

The next day the test is repeated; the little tree lies in exactly the same place as on the day before at the beginning. Tschego uses a bundle of straw as a substitute for the stick, and, when it proves too soft, folds it double just as in the first test, making it also stiffer. This time, even after folding it, it still remains too flexible, so she hastily repeats the proceeding, and the bundle, now composed of four folds, thus becomes extremely firm. But now it is too short, and Tschego tries to squeeze the whole tree through the bars. As, of course, she fails in this also, she returns to the straw, and, after many failures, finally sits down quietly. But her eyes wander and soon fix on the little tree, which she had left lying a little way behind her and, all of a sudden, she seizes it quickly and surely, breaks off a branch, and immediately pulls the objective to her with it. This proceeding has no relation to her former attempts to push the tree through the bars. While breaking off the branch, Tschego turns one side towards the bars; the little tree does not touch them at all and is neither treated as a whole nor moved towards the bars; nothing else is involved, but just the breaking off of the branch.

In this experiment, what is particularly worth noting is the fact that, for a long time, not the slightest sign was given of the expected solution; when the branch is suddenly broken off, the proceeding goes on, without any "hiatus," to the reaching out with the stick thus created; both actions together make one united proceeding.

The second experiment is one performed by Tolman and Honzik.⁽²²⁾ This experiment was done with rats. The apparatus is a form of the elevated pathway type of maze, that is, the alleys are formed by strips of wood without side-walls. These strips are raised a sufficient distance from the floor so that the rat will not attempt to jump off.

The diagram of the maze is shown in Figure 55. The gate is arranged so that the weight of the rat upon it will cause it to lower and allow the animal to go through. However, as soon as he is through, it closes again so that he cannot go back.

The animals are given preliminary training in the apparatus in order to accustom them to the experimental situation and also to set up in them preferential tendencies with reference to the three pathways to the food.

Rats as a rule will learn rather quickly to take the shortest pathways to food when several pathways of various lengths are presented to them. Consequently, in this experiment, the animals will soon learn to prefer Path 1, of

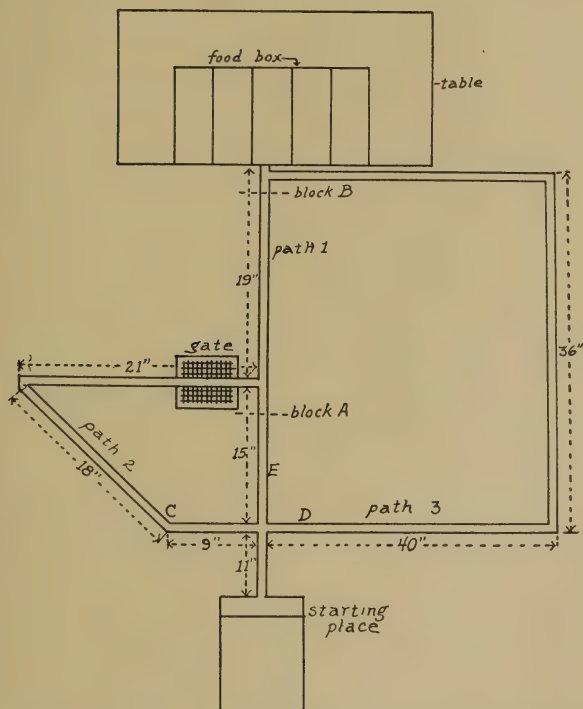


Fig. 55.—Ground Plan of Elevated Maze Used by Tolman and Honzik. (See text.)

the three possibilities. In order to force them to take one of the other pathways, it is necessary to put in Path 1 block A. This forces them to return to the bifurcation of the paths and to take either Path 2 or Path 3. Of these two, the rats will prefer Path 2. This is shown by the fact that of a total of 1,357 runs made by the 15 rats with block A

in place, 1,229 (90.57 per cent) were by Path 2, and the remainder by Path 3.

We have at this point, then, the following situation: if the rats are put in the maze without blocks of any kind, they will in the vast majority of cases take Path 1; if, however, Path 1 is blocked at *A*, they will in the majority of the cases take Path 2. We are now ready for the crucial test trial to determine whether the animals show insight. This is done by removing block *A* and putting in block *B*. The animals will run to block *B* over Path 1, but they will, of course, have to return to the bifurcation of the paths. The tendency, as indicated above, is now to take Path 2. However, if the animals show insight into the situation, they will take Path 3, because under these circumstances, with the block at *B*, Path 2 is also blocked so far as getting to the food is concerned. The results show that 14 of the 15 rats took Path 3.

At this point, let us take the following quotation from the authors' report:

If the taking of Path 2 or Path 3, after return from block *B*, were a matter of pure chance similar to the tossing of a coin, the probability of 14 out of 15 rats taking Path 3 and 1 rat taking Path 2 would be .00046. The actual result of 14 rats taking Path 3 and 1 rat taking Path 2 on the first test run indicates, therefore, a very decided "loading" in favor of Path 3, in spite of the fact that the "loading" during the training period was just the reverse, viz., in favor of Path 2.

This "loading" must consist in the ability of the animal to grasp the relationship of the position of block *B* to the commonness of Paths 1 and 2 at this point. That is, the animal shows "insight."

It should be emphasized that this experimental set-up allows the animal to survey the total situation, since there are no side walls on the maze. Tolman and Honzik⁽²²⁾ also used a maze of a similar pattern with side walls and a similar experimental procedure, with negative results.

Thus, support is given to Köhler's contention that the animal must be allowed to survey the total situation if it is to be expected to grasp relationships.

Reasoning

This term has come into the literature of experimental animal psychology chiefly through the work of Maier.^(16, 17) He states, "The term *reasoning* implies that something new has been brought about, and that in some way, past experiences have been manipulated. It therefore seems that behavior patterns made up of two isolated experiences characterize what is meant by behavior which is the product of reasoning."⁽¹⁶⁾

With this statement as a basis from which to start, let us examine two of Maier's many experiments. The first experiment is one in which are used three tables, all of which differ from each other in several respects. These tables are connected by elevated pathways, as shown in Figure 56.

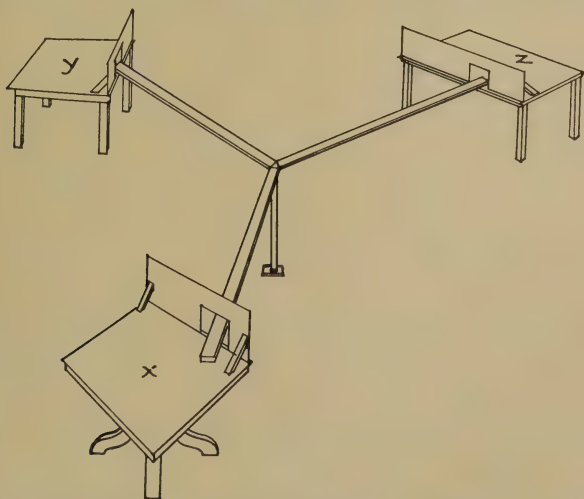


Fig. 56.—Diagram Showing Arrangement of Tables in Maier's Experiment on "Reasoning."

The rat is allowed an opportunity to explore this situation and to run from one table to another over the pathways, thus becoming familiar with the experimental situation. This period of exploration is called "Experience 1."

The animal is now removed to one of the tables (for example, *X*, Figure 56) and fed a small amount of food on that table. This is "Experience 2." It is now removed to one of the other tables, perhaps *Y*. Now if the rat combines "Experience 1," that is, knowledge of the pathways, with "Experience 2," it will go directly from Table *Y* to Table *X*, where it has just been fed and where it will receive more food. The problem can be varied from trial to trial by giving the preliminary food on different tables and also by starting the animal from different tables.

Another experiment of a more complex nature was also used. The layout of the experimental situation in this case is shown in Figure 57.

A and *B* represent the two halves of a large table. These halves are separated by a cardboard partition (*o-p*) over which the rats, with difficulty, may scramble. A maze of the elevated pathway type starts in the small box at point *X* and ends in the wire cage at point *Y*. Before, however, this maze and the box and cage are connected to the table, the rats are allowed to thoroughly explore the table-top and to learn to scale the partition. When this is accomplished, they are taught the maze by being put in the box at *X*, from which they are allowed to run to the food in the cage at *Y*.

When this learning is accomplished, the rat is placed on the table at point *M*, with the food, of course, inside of the cage. This begins the test trial. As would be expected, the animal will spend a good deal of time trying to get into the cage. This, however, is impossible. Eventually, the animal will scale the wall, and now comes the critical point. Will the animal run directly over to the box at *X* and enter it in order to get on the maze, so that it may run

around to the food at Y? Maier found that his rats did go almost directly to the box, after they had scaled the wall. They scrambled into the box, although they had never entered the box before on their own initiative, and ran around the maze to the food.

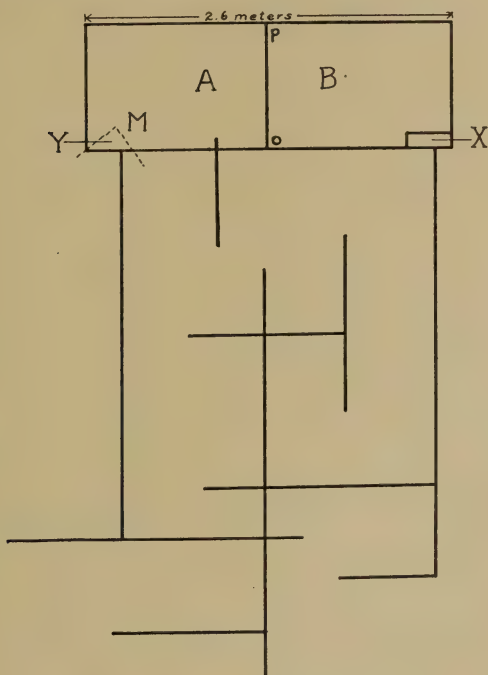


Fig. 57.—The combination of table and maze used by Maier in experiments on rats. The table is divided into halves A and B by the partition o-p.

These experiments show that the lowly rat is capable of a more intelligent type of behavior than perhaps one would be led to expect had he always observed this animal in the conventional maze or problem box situation. However, it is not clear that we need both the terms *insight* and *reason-*

ing. Apparently, these two terms indicate the same type of activity, if one may judge from the kinds of problems used to demonstrate the two. The ability to react upon the basis of relationships seems to be characteristic of both "reasoning" and "insight."

The Use of Tools

The use of tools has generally been considered one of the outstanding achievements of the human being. At the time at which this is written, the world is in an economic maelstrom, one cause of which, so some people say, is the intemperate production and use of tools. We are said to be living in the "machine age." Whether all this is true or not, the fact remains that man is a tool-using animal. The question for the animal psychologist is to determine whether and to what extent this ability is found in the lower animals.

It might be well to start with an attempt at a definition of tool. For the purposes of this discussion, we will define a tool as any manipulable object that is used by the animal as an intermediary link between itself and its objective. Using the term *tool* in this fashion, it is apparent that tool-using is widespread among animals. Some examples are: the use of wood shavings to secure water by the rat (Fritz ⁽³⁾); the use of a lever by cats to secure food that was placed upon one end of the lever by the experimenter (Adams ⁽¹⁾); and the use of boxes or other objects by apes to secure food that is otherwise out of reach (Köhler ⁽¹³⁾). These are just a few examples. They could be multiplied almost indefinitely.

However, these various examples do not necessarily indicate the same ability in the different species of animals. For example, let us consider the case of the cat that moves one end of a lever in order to get the food that has been placed upon the other end.

In this case, we have the tool made and put in position by the experimenter. If the cat had been left to its own devices, even though there had been plenty of material (for example, sticks, and the like) from which to construct a lever, it probably would never have obtained the food. Contrast with this the behavior of the chimpanzee, Tschego, described by Köhler and quoted above (see page 337). In this case, we find that the animal actually constructs a tool as well as uses it. This ability to contrive may be only a higher degree of the ability to use, or it may be a qualitatively different ability. That question we are willing to leave open, and we shall content ourselves with the recognition that there is a difference.

Delayed Reaction

The delayed reaction experiment was suggested by Carr. It was Hunter,⁽⁸⁾ however, who put the suggestion into effect and who wrote the now classical monograph on delayed reaction. The experiment was devised to test for ideational ability. We should prefer, however, to use the phrase "representative factors" instead of "ideational ability." The meaning of these terms will become evident as we describe the delayed reaction experiment.

The essential principle of this experiment is to present the animal with a stimulus to which he habitually or instinctively reacts, then to withdraw the stimulus and allow the animal to make the reaction in its absence. The thought is that since the stimulus is absent at the moment of reaction, the animal must react to some substitute for that stimulus, and thus the term "representative factor."

There are two general methods for testing delayed reaction, and both of them were used by Hunter. They are the indirect method and the direct method.

In the case of the indirect method, the experimenter has to set up in the animal an association between the stimulus

and the reaction before he can start on the delayed reaction experiment. In Figure 58 is given the ground plan of

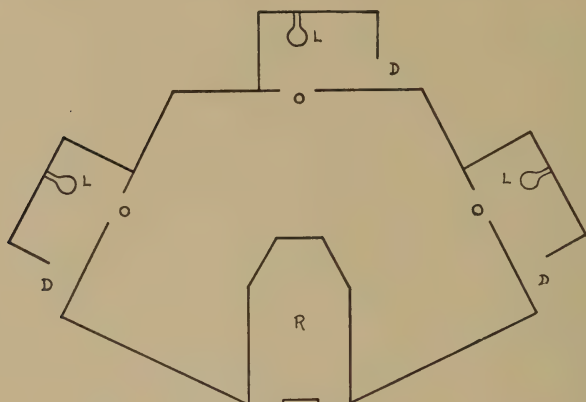


Figure 58.—Simplified ground-plan drawing of delayed-reaction apparatus used by Hunter. A light *L* may be made to shine through either of the openings *O*. When the animal goes through the lighted opening, he will find food at position *D*. The animal is inserted in box *R*, which has glass sides so that he can see which opening is lighted. If the animal attempts to go through an opening that is not lighted, he will find his path obstructed by movable blocks (not shown here).

the three-choice apparatus that Hunter used with his animals. In this particular experiment, light was used as the stimulus. The animal was taught to go to the lighted opening to get his food. That is, the lighted opening becomes the signal for food. When the animal has learned this association, a light at one of the openings is turned on and then off while the animal is still confined in the release cage. After a given interval of time has elapsed, it is released so that it may be determined whether it can go immediately to the door that it has last seen lit. Of course, the light is not at the same door every trial, and the animal does not react correctly by learning to go always to a certain door.

In the case of the direct method, the animal already

reacts to the stimulus because of its hereditary constitution or past experience. Therefore, the experimenter need not spend time in the preliminary training forming this association. Hunter used this method with some of the children that he studied. He set three boxes before the child. He then let the child see him drop a favorite plaything into one of the boxes. The child's attention was then otherwise engaged until a given amount of time had elapsed. It could then approach the boxes, the test being to determine whether the child could reach into the box into which it had seen the plaything dropped. It was, of course, not allowed to see into the boxes. This direct method can be successfully used with the higher animals such as monkeys, apes, and man, but it is not very practical with animals lower in the scale.

With this rather long introduction to make clear the methods used, we may turn to the results. There are two important questions to be considered. First, what is the maximum interval that may separate the presentation of the stimulus and the reaction without seriously decreasing the correctness of the reaction? Second, how is the animal able to bridge the interval, that is, what "representative factors" does he use?

Let us discuss the question of length of delay first. It is very difficult to summarize the data on this question because the length of delay is affected by so many factors. Let us consider some of these factors and their influence.

In his experiment that is described above, Hunter found that the maximal delay for the rat was ten seconds. In an experiment by Honzik,⁽⁵⁾ the rat was shown to be able to delay for at least forty-five seconds. Honzik's apparatus is shown in Figure 59. In this apparatus, a white curtain indicates the correct door, and the incorrect doors are covered by black curtains. Comparing the two experiments, this is probably a difference of minor importance.

A second difference of much greater significance, how-

ever, is the fact that the animals were allowed to run towards the white curtain in their delay trials. They could not, however, in these trials, push aside the curtain, because it was backed by a wooden block. As soon as an animal had made the reaction to the curtain, the screen was lowered and a black curtain substituted for the white one. At the end of the delay period, the screen was raised.

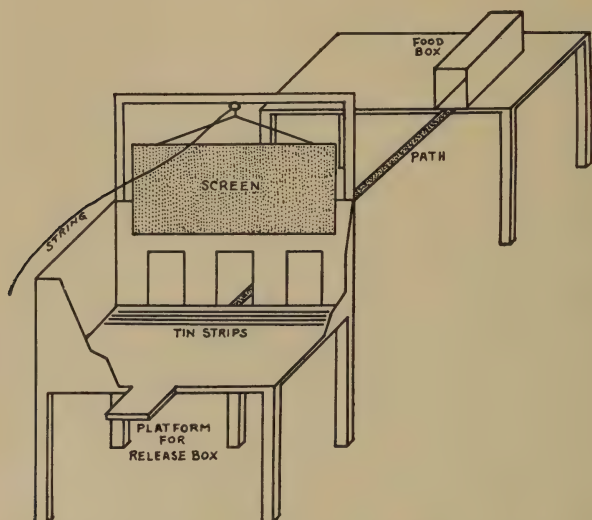


Fig. 59.—Delayed-reaction apparatus as used by Honzik. The path to the food box shown leading from the middle door can, of course, be moved to any of the three openings. The tin strips were used to give the rats an electric shock if they made an incorrect response.

If the animal could in some way remember where he had last seen the white curtain, he would be able to make the correct reaction.*

Honzik believes that this running toward the stimulus in

* Of course, a series of delay trials must be given, so that one may determine whether the animal is making correct reactions above that which would be expected by chance.

the delay trials gives the animals the following advantages:

[1] It could be made certain that the rat had actually received the stimulus and [2] this running toward the stimulus would probably also reinforce the stimulus and hence enhance the animal's ability, after the delay, to react correctly to the place where it had been.

Loucks⁽¹⁴⁾ has performed an experiment on "delayed alternation." He used an apparatus similar to the Hunter temporal maze (Figure 58, page 346). In this apparatus, he required that the animal learn the simple alternation, that is, R L R L or L R L R, depending upon which way the animal turned on the first trial of each day. Now it is obvious, of course, that the animal can be delayed, in between the trials, and since there are no differential cues in the external environment, it must remember which way it turned on the last trial in order to be able to turn correctly in the present trial. The cue received by the animal from the preceding trial differs, of course, from the cues used by Hunter and Honzik in that it is something intrinsic within the animal, and not imposed upon it from an outside source, for example, light. Loucks was able to use delay periods as long as five minutes.*

* Hunter maintains that the simple alternation problem cannot be used as a delayed reaction situation unless the regular sequence of turns is destroyed. By the nature of the alternation problem, this method is, of course, impossible. The present writer believes, however, that the same principle is involved in both types of situations. He does not understand why the fact that there is a regular sequence of turns militates against the necessity for the animal to carry over from one turn to the next some sort of a factor that determines its behavior, so long as there are no differential external cues present at the time of response. It is true, of course, that in the usual delayed reaction experiment, the differential cue (light, for example) itself cannot be carried over, since it is removed by the experimenter. In the alternation problem, this cue is internal to the animal and therefore cannot be unequivocally removed by the experimenter. However, the experiment by Loucks at present under discussion bears upon the point. See the future discussion of this experiment under "Methods of Bridging the Interval."

Maier ⁽¹⁵⁾ taught rats to run up inclined paths from a floor to a table-top for food. There were three of these paths, one of which he would allow the animal to traverse three times in succession. The animal was then removed to an adjoining room. At some later time, the animal was returned to the table-top and allowed to run to the floor by a fourth path. The object was to see whether the animal could go around to the path that it had used in the last three trials and go up it to get food. Maier found that the animals were able to accomplish this after the elapse of several hours.

He called this delayed reaction. If it is accepted as such, the length of delays that he used successfully are the longest ever recorded for the rat. However, Tolman ⁽²¹⁾ has pointed out, we believe correctly, that this is not delayed reaction in the usual sense of the term, since the rat experiences the total situation, just preceding the delay, and not just a sign (for example, light) that signifies the total situation.

With animals higher in the phylogenetic scale than the rat, longer delay periods can, as a rule, be used successfully. In the case of Hunter's experiments, the dog was capable of maximal delays of five minutes, and the raccoon responded correctly with a delay of twenty-five seconds. The older children were capable of delays of at least twenty-five minutes. It is quite probable that all of these animals would be capable of longer delays under other conditions.

Adams ⁽¹⁾ received correct responses from cats after delays ranging from three to seventeen hours. The longest delays with correct response with animals below man have been found with monkeys and chimpanzees. Using the direct method of hiding food in the presence of animals, Yerkes and Yerkes ⁽²⁶⁾ found a delay of forty-eight hours with correct response with the chimpanzee, and Köhler, ⁽¹³⁾ with the same species, found a delay of sixteen and one half hours with correct response. Tinklepaugh, ⁽¹⁹⁾ working with mon-

keys, found them able to respond correctly after delays of from fifteen to twenty hours.

Methods of Bridging the Interval

The above brief summary of the results with reference to the length of delay indicates that there is a rough correlation between the position of the animal in the phylogenetic scale, and the length of the interval that may elapse between the stimulus and the reaction without seriously affecting the accuracy of the latter.

This fact is of great interest, but the question of how the various species bridge the gap is perhaps of much greater significance, although, at the same time, the answer is much more difficult to discover.

However, we have some experimental data that are relevant to this inquiry. In Hunter's experiment, the rats and the dogs kept a gross bodily orientation. When the light was flashed, they would either orient their whole bodies or their heads in the direction of the light, and during the delay period they maintained this orientation. When they were released, they simply followed their noses, so to speak, and thereby were able to go to the correct box. If this orientation was disturbed during the period of delay, the animals were unable to react correctly. The raccoons and the children, on the other hand, did not have to maintain this orientation in order to react correctly. This fact led Hunter to venture the theory that raccoons were capable of "sensory thought," or what is perhaps more commonly called "imageless thought." He indicates that this is a lower type of ability than thought with images, which, of course, he will concede to children.

However, it has been shown since Hunter's experiment that even a rat is able to make a successful delay without this gross bodily orientation. These results were obtained by Honzik ⁽⁵⁾ and McAllister, ⁽¹⁸⁾ among others. Walton ⁽²³⁾

has shown also that the dog need not keep his orientation in order to delay successfully. Likewise, the apes and monkeys rarely, if ever, maintain a gross bodily orientation during the period of delay.

However, there is another kind of bodily orientation that would not be apparent to the experimenter, and that would therefore escape notice, although it might conceivably be used by the animal. This orientation would consist in the maintenance of a muscular tension. The muscle in which the tension would be maintained would vary with the position of the stimulus. It is apparent that the device would have to be such that it would not necessarily be disturbed by a shift in the gross bodily orientation, since at the moment of response the animal must necessarily be oriented with reference to the apparatus as he was when he received the stimulus.

It is hardly conceivable that a device of this sort could be used successfully to bridge the long delays with correct response that are found with the primates. However, with the rat, the longest delay with correct response has been a few minutes at the most (Maier's work excepted). Under these conditions, it is conceivable that it might work very well.

In order to test this hypothesis, Loucks⁽¹⁴⁾ gave his rats a general anæsthetic during the period of delay. If there was a muscular tension involved, it certainly would be destroyed by the relaxation of the muscles caused by the anæsthesia, and therefore the animal would be unable to make correct responses. However, it was found that the rats could respond correctly after the anæsthesia. McAllister⁽¹⁸⁾ likewise caused the animals to dig through sand during the period of delay, on the supposition that this activity would make it difficult to maintain a muscular tension. He found that the animals could react correctly under these conditions. It is apparent, therefore, on the basis of experimental results, that the evidence is very much against

the possibility that the maintenance of a differential muscular tension is the device used by the rat to bridge the delay in delayed reaction experiments.

Experimentation has also shown that different animals of the same species may rely upon somewhat different factors in their reactions to delayed reaction situations. Tinklepaugh,⁽¹⁹⁾ for example, presents evidence to show that one of his monkeys (Cupid) tended to make his choice of the container under which food had been placed, in his presence, on the basis of the relation of that container to himself, while his other monkey (Psyche) apparently oriented the container with reference to points in space and independently of her own body.

Some inkling concerning the limitations of the chimpanzee is given in the work of Yerkes and Yerkes.⁽²⁶⁾ They used four boxes, each of a different color and each placed in a corner of a square room. The chimpanzee was located in the center of the room and was allowed to see food dropped into one of these boxes. Under these conditions, it could respond to the correct box after a period of three hours. The animal was removed from the room during the period of delay.

However, if the boxes were interchanged in position during the absence of the animal, so that it would be compelled to make the reaction on the basis of color rather than position, the maximal delay with correct response obtained was thirty minutes. Furthermore, in the beginning, the animal was incapable of adequate adjustment to the situation and reacted in one of the following ways: (1) on the basis of position, (2) on the basis of the box from which it had obtained food in the preceding trial, and (3) on the basis of perseverational response either by choosing the box of the same color in trial after trial or by repeatedly rejecting or avoiding a given color.

The authors also give the following interesting account of the behavior of the chimpanzee in this connection:

In the initial series of experiments, when absolute and relative positions were constant and the animal always found the food where it had seen it placed prior to the interval of delay, response was made immediately with evident ease and certainty, and usually with slight evidence of visual observation of the boxes. But when the conditions were so altered that color became the only constant factor, and the sole basis for correct response, the attitude of the subject changed completely, and in place of carelessness of observation, immediacy, and certainty of response, there appeared observational scrutiny, comparison, often recognition, hesitation, delay, and occasionally vacillation; expressions of disappointment, incredulity, mystification; expressions of resentment, anger, depression, and finally in some instances refusal to choose.

An account of delayed reaction would certainly be seriously lacking if no mention were made of the experiments recently done by Tinklepaugh ⁽²⁰⁾ on multiple delayed reaction. In one part of this experiment, he used ten pairs of containers, one pair in each of ten different rooms. With the chimpanzee in the room and watching the process, food was placed under one member of the pair. The experimenter and the chimpanzee then proceeded to another room, and the procedure was repeated in each room until all the rooms had been entered. The animal was then led back to the first room and allowed to choose one of the containers; then to the next room, where he was allowed to repeat the act; and so on, until he had chosen a container in each room. Under these conditions, one chimpanzee (Bill) made 92 correct choices out of 100, while another (Dwina) made 88 out of 100. The animal did not need to return to the rooms in the same sequence in which they had observed the placing of the food in order to make correct responses.

Two monkeys were used also in this experiment. However, in their cases, only five pairs of containers were used. They made 78 and 80 per cent correct choices. Tinklepaugh made the following interesting observation:

The behavior of the monkeys was decidedly different from that of the chimpanzees. Though eager to make their responses each time after they saw the food placed in a given situation, as soon as they were taken away from the immediate vicinity, their interest turned to cracks in the floor or the partitions or to any knot hole or stray bit of dirt or refuse which happened to be in their route. Any sound in an adjoining room or within their range of vision distracted them. They never seemed to connect up and hold the series of settings as a part of one task as did the chimpanzees. This difference was best shown when a subject was given entire freedom after a series had been set. Either of the chimpanzees, when released in this manner, would rush from one room to another, making his choices and securing his food. The monkeys would respond to any pair of containers which came into their view as they ran about, but they never went consistently from one pair to another unless they were led.

Because of the fact that there were only ten available rooms in the laboratory, Tinklepaugh did the second part of his experiment with a different arrangement. On this occasion, he arranged sixteen pairs of containers in a circle in one room. The chimpanzee was seated in the center of the circle and saw the experimenter place food under one member of each pair. Then, going to one pair at a time, the animal was allowed to choose one of the containers. Under these conditions, the two chimpanzees each made about 78 per cent correct responses. Four boys ranging in age from seven to nine years also were used in this experiment. They made 67, 58, 62, and 64 per cent correct responses, respectively.

When the two monkeys were used in the experiment, they experienced the same degree of difficulty with three pairs of containers that the apes did with sixteen pairs.

The Double Alternation Problem

We have had occasion to mention several times the simple alternation problem in the temporal maze (on page 325 is shown a ground-plan diagram of the apparatus.) It will be remembered that in the simple alternation prob-

lem, the animal is required to make in succeeding trials the following sequence of turns: R L R L, and so forth.

Hunter also has used the double alternation, in which the endeavor is made to teach the animal the R R L L R R L L sequence of turns.

A little consideration will show that there is a significant difference between the simple and double alternation problems. In the former, a turn to the right presents a cue to the animal that in some ways determines his turn to the left in the succeeding turn. Likewise, his turn to the left presents cues that determine his turn to the right in the next trial. In the latter, the turn to the right must at one time present cues to turn to the right, and at another time (the second, for example) it must present cues to turn to the left. This is, of course, impossible, as we cannot have the same causes producing two different effects. The same situation obtains for the turns to the left.

Under such conditions, therefore, if the animal is to learn the double alternation problem, he must supplement the cues received on his tours by some other factor, or factors, that may act in a differential manner. Hunter ⁽⁷⁾ suggests the following possibilities: There may be (1) a cumulative piling up in the nervous system of the retained effects of the responses already made, or (2) a symbolic process: "As, for example, the human subject would have no difficulty with double alternation, if he supplemented his responses with the verbal behavior, 'It is two, two. I first go two right, then two left, etc.' "

Hunter is inclined toward the latter hypothesis. In his original work with the rat,⁽⁹⁾ he found that this animal could not learn the double alternation problem even with the smallest possible number of trials in the series, namely, R R L L. He had already found that the rat could not do the delayed reaction experiment unless it kept the gross bodily orientation. In the later experiment,⁽⁷⁾ he found

that raccoons could do the double alternation to the extent of R R L L, but could not extend the series to R R L L R R L L. He is inclined, therefore, to believe that the raccoon, but not the rat,* can use a symbolic process.

Gellermann⁽⁴⁾ has extended the work on double alternation in the temporal maze to monkeys and human beings. He finds that monkeys can learn the R R L L series. In a modification of the method in which two boxes are used instead of the maze, with the food placed two times in the right and two times in the left, the monkeys can extend the alternation beyond the training series, which in this case included eight trials per series. The animals were able to extend this to sixteen trials per series. The box apparatus was used because a monkey does not readily move in a maze.

It goes without saying, of course, that the human child readily learned this type of response. Furthermore, Gellermann states that "human subjects formulate their solutions of the double alternation problems verbally in the general form, 'twice to the right, twice to the left,' etc. This formulation supplements nondifferential interoceptive and exteroceptive stimuli encountered within the temporal maze, to call out the double alternation response."

The Multiple Choice Problem

In Chapter X, we had occasion to mention and describe the multiple choice problem in connection with the various

* As it has been shown since Hunter's original experiment that rats can delay their reactions without gross bodily orientation, see, likewise, the report by Hunter and Nagge,⁽¹⁰⁾ who have secured some evidence to indicate that rats are capable of performing the double alternation problem. The animals did this, however, only after a long series of preliminary trials in an apparatus involving an R R L L sequence of turns, but with differential external cues to determine each response. There was no unambiguous evidence that the animals could extend the series beyond the R R L L sequence, upon which they had been trained.

methods that have been devised for the study of learning. As we have already mentioned, this problem was devised for testing ideation in animals. As soon as the animal understands the system that the experimenter uses in the manipulation of the doors, it should have no further difficulty with the problem. This point in the animal's learning may be evidenced by a sudden drop in the learning curve.

Yerkes ⁽²⁴⁾ in his work with an orang-utan, Julius, on the multiple choice problem, in which the animal was expected to learn to choose the first open door to the left of the series of open doors, found this sudden drop in the learning curve. In this connection, he says: "The curve of learning plotted from the daily wrong choices . . . , had it been obtained with a human subject, would undoubtedly be described as an ideational, and possibly even as a rational curve; for its sudden drop from near the maximum to the base line strongly suggests, if it does not actually prove, insight."

Yerkes and Yerkes ⁽²⁵⁾ expressed the belief that the multiple choice type of problem was one that could be used successfully with different species of animals in order to give them a rating on a more or less standard scale, that is, with respect to the ability or abilities needed to solve this problem. In this connection, a number of species of animals have been tested. Washburn gives a summary of the results. In the last one and a half decades, however, the experimentation on this type of problem has not been pushed as vigorously as that on the delayed reaction and the double alternation problems. As yet, we cannot unequivocally rank animals in the phylogenetic scale according to ability.

It should be noted, also, that while "insightful" learning may possibly be demonstrated by the multiple choice technique, the technique does not conform to the requirement laid down by Köhler for his roundabout procedures in that

the relationship or principle to be grasped is not within the perceptual field of the animal.*

Judgment

It has been found that rats, when presented individually with an equal number of large and small sunflower seeds, will tend to eat more of the large than of the small (Yoshioka ⁽²⁸⁾). This fact was interpreted as a judgmental response on the part of rats—a judgment that large seeds hold a greater amount of food material than do small ones.

Tolman questions whether this should be accepted as being really a judgmental response unless it can be shown that after repeated experience with the two sizes of seeds the rat will give up its preference, because, as a matter of fact, the large sunflower seeds do not contain more edible substance, and furthermore, they require more time to crack and eat.

In a second experiment, Yoshioka ⁽²⁷⁾ has shown that the preference does disappear with continual experience, and that the preference may be reversed if the experience is repeated a sufficient number of times and the rats are tested under “conditions where deliberate choice is made possible.”

It seems questionable whether this size preference for food necessarily involves very much of the process of comparison and weighing of two or more possibilities that we usually regard as judgment in the case of the human being.

Something more like the behavior we could call judgment in the human being is indicated in the experiments by Klüver ⁽¹²⁾ on monkeys. Each of his animals was presented with two strings that were attached to boxes that could be pulled to the animal's cage. One of the boxes had a 325-gram weight in it and the other a 250-gram weight. The

* It is interesting to observe, however, that Yerkes ⁽²⁴⁾ used many of the problems that Köhler described in his *The Mentality of Apes*. Several private communications passed between the two men, but because of the World War, they were largely isolated from each other.

heavier box contained food and the lighter one did not. The monkeys had had previous experience with this type of situation, but on those occasions, the boxes differed more widely in weight. Klüver describes their behavior thus:

In observing the reaction to the 325 g. : 250 g. pair we could not fail to be impressed with the great efforts made by the monkeys in each trial. Instead of merely pulling in a box, they compared the boxes back and forth. The perseverance displayed in these comparisons was truly remarkable. The work of most days meant making hundreds of displacements, but no weakening of the tendency to compare was ever observed. . . . The great number of comparisons was undoubtedly indicative of the great uncertainty of the monkeys. This is in harmony with the fact that a fairly stable errorless performance was not obtained. The monkeys apparently had no difficulty in *comparing and relating* two weights; they only had difficulty in discriminating the weight *relata* which they were confronted with. At the end of the training period, the stimulus situation, it seems, was not "articulate" enough to call forth a consistent response in terms of the "heavier-than" relation; the comparison method, however, had become more and more independent, in fact, autonomous. One might say that at times there was nothing left but the mere technique of comparing, a technique not applied to any material. It happened often that only the ground near the two strings of the boxes was alternately touched in rapid succession. It also happened frequently that the comparison of the boxes was preceded by "pseudo-comparisons" of the strings, that is, by merely touching the strings without pulling them taut. . . . Although, in a given trial, as many as ten or more comparisons were often made, the actual displacements of the boxes became less and less. Especially in the case of G.-R.* It was observed that a pull often resulted in a displacement not larger than 1 centimeter, sometimes merely in pulling the string taut. In a number of instances, G.-R. grasped the string of the left box with his left hand and, at the same time, the string of the right box with his right hand, and, by merely pulling the strings taut successively, made his choice. It even happened that he pulled both strings taut at the same time or that he displaced both boxes simultaneously before moving them successively.

This description of the behavior of the monkey certainly reminds one of the behavior of the human being in making

* The designation of one of the monkeys.

a judgment of which of the two weights is the heavier in cases where the difference in the weights approaches the differential limen.

Abstractions and Generalizations

The question to be considered here is whether an infra-human animal is able to abstract from a number of somewhat similar situations an element or several elements to which it will learn to make a reaction in such a way that if it is presented with a new situation containing these elements, it will react in essentially the same way that it did in the training situations. If it is capable of doing so, we are justified in stating that the animal has formed a concept.

The question of whether the animals below man are capable of conceptual learning has intrigued students of animal behavior for a long time, but it is only recently that we have had a sufficiently systematic investigation of this point.

The essential nature of concept formation in the human being will give us the cues concerning the direction that experiments in concept formation in animals must take. Fields ⁽²⁾ paraphrased a quotation from Hull ⁽⁶⁾ that so clearly states this process in the human child that we will quote it:

A young child finds himself in a certain situation (white equilateral triangle, apex up; area, 28 square centimeters), reacts to it by approach, and hears it called "triangle." In a somewhat different situation (white equilateral triangle, apex down; area, 28 square centimeters), he hears that called "triangle." Later, in a still different situation (black equilateral triangle, rotated 30 degrees; area, 55 square centimeters), he hears that called "triangle" also. There is no obvious label as to the essential nature of the situation, which precipitates at each new appearance a more or less acute problem as to the proper reaction. And so the process goes on with right-angle, isosceles, and scalene triangles, until the day finally comes on which the child makes the specific language response, "triangle," whenever any of the foregoing classes of figures are presented. This child now has a meaning for the shape

"triangle." Upon examination, this meaning is found to be actually a characteristic more or less common to all triangles, and not common to squares, circles, etc. But to the child, the process of arriving at this meaning, or concept, has been largely unconscious. The formation of the concept has never been an end deliberately sought for itself. It has always been the means to an end—the supremely absorbing task of physical and social reaction and adjustment.

If this is the way in which the child learns a concept, how must we proceed in investigating conceptual learning in animals? Obviously, we cannot use the language response in the case of the animal; but is this necessary? Not at all. We may easily substitute another type of response, for example, an approaching response. Let us assume now that we are to determine whether an animal can learn a concept of triangularity. We will then present the animal with a triangle and some other shape, a circle, for example, to be discriminated from it. When the animal learns this discrimination, we perhaps rotate the triangle slightly and again establish the discrimination. Then the triangle is rotated a few more degrees and the discrimination again established, and so on with many changes in the triangle in many respects, such as size, brightness, color—if the animal has color vision—shape, and so forth. When the animal has learned to react positively to all these triangles, we present to him figures that he has never experienced before but that include the characteristics of triangularity, for example, three small circles arranged in the form of a triangle, one circle at each corner. If the animal continues to react positively to these figures without further training, we assume that it has formed a concept of triangularity and, from the many experiences he has had, has generalized it into a concept.

The above procedure is essentially that which Fields ⁽²⁾ used with the rat as a subject, and he comes to the conclusion, "When white rats are given a training period specifically designed to provide a large number of different 'triangle

experiences,' the rats are able to perfect a type of behavior which is fully described by the implications inherent, in our case, in the term 'concept.' "

Although Klüver ⁽¹²⁾ does not do so, we believe that a similar conclusion could be drawn from the results of his experiments, by his methods of "equivalent stimuli." *

It should be noted that other experiments also might be used to indicate that animals are capable of abstractions: for example, the experiments showing that animals will react to relationships—experiments in which the animal is shown to react to "larger than" or "brighter than" relationships. The animal may be said to abstract such a relationship from the situation with which it is confronted in the training series in such a way that it will react on the basis of this relationship when confronted with the stimuli of a different absolute size, or brightness, and the like.

Conclusion

In this chapter and the preceding one, a few of the many experiments that have been performed in the field of animal psychology have been summarized. Sufficient evidence has been given, we believe, to indicate strongly to the reader that human learning behavior has its analogue in the behavior of the infrahuman species. The task of tracing the evolution of behavior is as absorbing to the animal psychologist as the task of tracing anatomical structures is to the zoölogist. May we hope that eventually the former task may be accomplished as thoroughly as the latter is being done?

In these two chapters, the writer has acted primarily as a *raconteur* and only secondarily as a critic. So long as the

* Klüver's position seems to be that it is little, if any, help in understanding an animal's behavior to attach labels to it. With this position the present writer is quite in agreement. However, the use of labels helps one in writing an exposition of this behavior, and in that way they serve a useful purpose, although they should not be taken seriously.

experiments are done under well-controlled conditions, there is little opportunity for critical discussion of the results. On the other hand, there may be and usually is very great opportunity for discussion of the interpretation of the results. The discussion of interpretation of results obtained from experiments on the learning processes, however, brings us into the realm of theory, and that realm belongs to Professor Tolman in the chapter which follows.

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CHAPTER XII

Theories of Learning

Formulation of the Theories and Their Adequacy
in the Light of Data Collected

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Facts of Learning

WE turn, in this chapter, to the theories of learning. But we shall find it helpful to our purpose first to review the facts of learning that have been presented in the immediately preceding chapters. We shall distribute such facts under four heads: (1) conditioned reflex learning, (2) sign learning, (3) trial-and-error learning, and (4) higher forms of learning. Let us briefly delimit these four classifications.

1. The rubric "conditioned reflex learning" will be used in this chapter to refer only to that selected aspect of the conditioning process which consists in the original unconditioned response becoming attached, as such, to the conditioned stimulus. For it is this part only of the total conditioning process that has been referred to by most psychological theorists when talking of the conditioned reflex principle.

Actually, of course, as Liddell points out (in Chapter IX), the total conditioning process usually seems to involve more than this new attachment of the original response. He says (see pages 279-280):

Pavlov selected only a single sample of the dog's total behavior in the conditioning situation for study: the quantity and rate of salivary secretion. . . . [But] the salivary response is *but one sample* of the highly intricate behavior of the dog in response to the signal that food is coming. A characteristic attentive posture is assumed, breathing is modified, and so forth. How unlike the dog's rigid posture when he expects food is his greedy plunging and vigorous gulping of the food when he is eating it! Although the secretory reaction of expectation is essentially identical with the secretory response to the eating of the food, the conditioned *motor* alimentary response differs radically from the unconditioned *motor* alimentary reflex. The two highly integrated acts of expectation and eating are quite dissimilar except for the common component of salivary secretion.

For the purposes of clearness in the theoretical argument, it seems to the present writer desirable, however, to distinguish such other features actually appearing in the conditioned reflex situation—such other new acts or phases of acts as appear in response to the conditioned stimulus in addition to the salivary secretion—and to refer to the establishing of these features as “sign learning.” Further, this concept of sign learning can then be used to cover *any* case, whether appearing in the conditioned reflex laboratory or outside of it, where an animal comes to respond in some new way to a second stimulus (that is, a “conditioned stimulus”) because of the latter's temporal or other regular concatenation with a first stimulus.

2. Sign learning is to be, then, our new rubric especially designed to cover instances that cannot be classed as true conditioned reflexes as we have just restrictively defined the latter. Everyday instances of sign learning would be cases where a man or animal has come to respond in some appropriate preparatory way to a characteristic sound-cue. Thus, my dog has come to react to the noise of my returning automobile before she can see the machine, and I find her already waiting for me on the sidewalk when I and the car finally loom into sight. She has learned to respond to the sound as to a “sign” for the car with me in it. Further,

the response which she has thus attached to the sign is not the same as the response she makes to the car itself when it and I finally arrive. The response to the sign is a preparatory coming forward; that to the actual car with me in it, one of scrabbling up and wet kisses.

3. "Trial and error" is the familiar name for the type of learning, described by Heron in Chapter XI, that consists in the selection of one from among an original array of alternative responses. The typical examples of problem box and maze were described by him in detail in that chapter. Before learning, the animal makes the "correct" response as one among a total array of initial "trials and errors." After learning, it is evident that this one correct response has been reinforced, while the others have dropped out.

4. The rubric "higher types of learning" will be used here, as it was by Heron in the chapter preceding this one, to cover the cases of so-called insight, reasoning, use of tools, delayed reaction, double alternation, and so forth. In all such instances, learning appears to involve something more than the mere formation of new stimulus-response connections or the stamping in and stamping out of old ones. The final response in all such cases appears rather as in some degree independent of present stimuli, and as controlled in part by temporally absent, or by indirect, relatively distant features of the total stimulus situation.

Finally, it must again be emphasized that these four rubrics, "conditioned reflex learning," "sign learning," "trial-and-error learning," and "higher forms of learning" are here used merely for cataloguing types of fact. Otherwise, confusion would slip in when we note that some of these very same names are used again to designate theories. Thus, we shall shortly discover: that not only are there conditioned reflex facts, but also a conditioned reflex theory; and that not only are there trial-and-error facts, but also a

trial-and-error theory. But let us turn now to the theories themselves.

Theories of Learning

There seem to be two main groups of theories, to be designated, respectively, as the *reflex-arc theories* and the *field theories*.

The reflex-arc theories are so called because they assume relatively neat, atomistic, and mutually insulated stimulus-response "connections." They assume that in learning, such reflex-arc connections are made and broken—"hammered in" and "hammered out." They subdivide further into two subordinate forms, *conditioned reflex theories* and *trial-and-error theories*. The conditioned reflex theories find the essence of all learning in the conditioned reflex facts. They assert that all the other apparently different types of learning really reduce, upon analysis, to conditioning. In a somewhat similar manner, the trial-and-error theories find the essence of all learning in the trial-and-error experiment, and they attempt to show that all the other kinds of learning are really, when analyzed, cases of trial and error.

The field theories may be dubbed the "Gestalt" and "near-Gestalt" theories. They assume that learning consists in some sort of a reorganization relative to an entire stimulus-field. After learning, the animal does not, according to these theories, merely make new responses to old stimuli. He makes such new responses because his whole perceptual and other cognitive adjustments relative to the entire stimulus-field have become fundamentally remade—reorganized—"regestalted." The field theories assume, further, that the laws underlying such a "regestalting" are more than merely the associationistic ones of repeated experiences. They assume that there are also laws involving "dynamic" principles of interrelation.

We must now examine each of these types of theory in detail.

Reflex-Arc Theories—Conditioned Reflex Theories

There have been many different proponents of the conditioned reflex type of theory. And each proponent has given the discussion his own peculiar stamp. No attempt can here be made, however, adequately to review all the resulting doctrines. We must be content with noting certain common features. And we may now consider this resultant common theory with respect to each of the four types of learning fact.

1. Conditioned reflex theories and the conditioned reflex facts.—This heading needs no discussion. Conditioned reflexes are, for the conditioned reflex theories, the ultimate fact. They explain themselves.

2. The conditioned reflex theories and sign learning.—The rubric "sign learning" was designed to cover all those cases in which, as in the conditioned reflex proper, learning consists in the fact that the animal comes to respond to a second stimulus that regularly precedes or accompanies a first stimulus, but in which, further, the acquired response to this second stimulus is not, as in the conditioned reflex proper, exactly the same as that made to the first stimulus. In sign learning, the new response expresses a type of "preparation." It is appropriate to the second stimulus as a "sign" for the coming or reaching of the first stimulus. (My dog comes forward in a preparatory fashion upon hearing the sound; she does not jump up and begin to kiss in response to the sound itself.)

The conditioned reflex theories have assumed, however, that such cases of sign learning reduce at once and without remainder to conditioned reflexes in the narrow sense. But as was just indicated, the difficulty is that in such sign learning, the responses that come to be made to the "con-

ditioned" stimuli are not the same as those made to the "unconditioned" stimuli. Several experimental instances where the attempt was made to establish conditioned reflexes but where all that resulted was sign learning will emphasize our point.

Wever ⁽⁷⁸⁾ sought to set up a conditioned breathing change in cats. The unconditioned stimulus was an electric shock. The conditioned stimulus was a tuning-fork sounded prior to and up until the giving of the shock. The breathing change in response to the unconditioned stimulus was a deep inspiration and expiration. But the change that finally appeared in response to the conditioned stimulus—the tone—was "an increase in rate of breathing, together with a marked decrease in amplitude." Wever called the latter characteristic a "flutter" response. In other words, whereas the unconditioned reflex was a deep inspiration and expiration, the "conditioned" reflex was a "flutter." In response to the actual shock, the cat took in a deep breath and rapidly let it out again; in response to the tone, which had become the sign for the shock, he merely "held" his breath.

A similar experiment was tried by Upton ⁽⁷²⁾ upon guinea pigs. He obtained similar results. But eventually, after sufficient training, Upton did succeed in establishing not merely the "flutter," but in addition, a deep inspiration and expiration following the "flutter." The occurrence of the "flutter" would in our terms be sign learning, whereas the subsequent deep inspiration and expiration would be the true conditioned reflex.

Warner ⁽⁷³⁾ sought to establish conditioned reflexes in rats, but succeeded in obtaining sign learning only. The following is a typical one of his experiments. The rat was placed upon two horizontal metal bars hung two feet or so from the ground. The unconditioned stimulus was an electric shock through the bars. The conditioned stimulus was a buzzer sounded for five seconds before the shock. The re-

sponse to the unconditioned stimulus was a wild "leaping off into space." The response to the conditioned stimulus was, on the contrary, that of "hanging for a moment, usually by the hind paws, and then dropping to the ground." It appears that the acquired response to the buzzer was one different from that to the actual shock.

In short, sign learning does not reduce to conditioned reflex learning. For conditioned reflex learning, the picture is:



Fig. 60.—Schematization of Conditioned Reflex Learning.

In this figure, S_b is the unconditioned stimulus, R_b the unconditioned response, and S_a the conditioned stimulus which eventually comes to bring out the same response, R_b . For sign learning, on the other hand, the new response which becomes attached to S_a is not the original R_b , but some sort of new response, R_a . Sign learning must be depicted, therefore, in some different fashion, perhaps as follows:

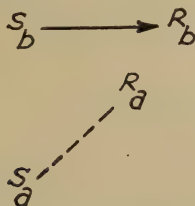


Fig. 61.—Schematization of Sign Learning.

We must conclude that the conditioned reflex theories are not, as such, adequate for sign learning.

Let us turn now to trial-and-error learning.

3. The conditioned reflex theories and trial-and-error learning.—Perhaps the first and best-known attempt to reduce a case of trial and error to the conditioning of reflexes

was that of Smith and Guthrie.⁽⁶⁰⁾ They took the case of Thorndike's kitten getting out of the puzzle-box. They assumed that the kitten is instinctively constituted to respond, when in confinement and hungry, to the sight of bars, cracks, corners, and so forth, by approach and attempted manipulation. If such features of the box prove, upon actual contact, immovable and rigid, then such approach and attempted manipulation will be superseded by turning away (retreat). But these turnings-away or retreats from all the rigid, non-movable features of the box after contact will, these authors say, sooner or later become "conditioned" to the visual stimuli that led to the preceding approaches. In this way, the cat will become conditioned to retreat as a result of the mere appearance of those features or parts that have proved rigid. Only the one feature, the door-opening device (button, loop or string, or whatever it may be), that *does* give way will not have such a retreat conditioned to it, and hence will continue throughout to bring out the original approach response and attempted manipulation. But the attack upon this one feature results in the door's opening, so that the cat will thereupon be attracted to a new stimulus—"open door"—and will respond to it by going out. He will then find food and eat. Approaching the button and approaching the open door are thus the only positive responses not followed by subsequent retreats. The visual stimuli coming from the button and from the open door will thus be the only ones that will have no retreats conditioned to them.

Our criticism must be that even if the above analysis were correct, it would succeed in reducing the learning of the puzzle-box not to true conditioned reflexes, but to sign learning. The conditioned non-attack upon the rigid parts of the cage are not the same as the original ceasing from actual bitings and clawings. Not to approach a given feature is hardly the same response as desisting or retreat from an actual biting or clawing. Rather, it is a respond-

ing to the visual appearance of the part as a sign for what would be found if that part were actually attacked.*

Frank,⁽¹¹⁾ Wilson,⁽⁸²⁾ Washburn,⁽⁷⁴⁾ Holt,⁽²⁰⁾ Hull,[†] and Spence⁽⁶¹⁾ have developed the conditioned reflex doctrine to cover not only puzzle-boxes, but also mazes. They continue to rely in part upon the Smith and Guthrie hypothesis, but they add new principles. They assume a conditioning back of the positive response to the final food. They also point to a persisting drive stimulus (for example, hunger) active throughout the whole performance. And they assume that the responses made to the different parts of the maze will become conditioned to the persistent drive stimulus more strongly the closer the animal is to the final goal. The latter principle, called by Hull the principle of the "goal gradient," is made to explain a number of facts. In the first place, it is made to explain why any blind becomes eliminated. The response of going into a blind always occurs prior to that of taking the alternative true path. Since, therefore, the latter occurs nearer in time to the final goal reaction, it is conditioned more strongly to the persisting inner drive and hence is learned at the expense of the immediately preceding blind entrance. Hull and Spence also show that the differences in strength between these conditionings to the blind entrance and to the going into the alternative true path should, according to the hypotheses, be less the farther away a chosen point is from the goal. This means that the later parts of the maze should be learned before the beginning parts. Actually, when other factors are ruled out, such a backward elimination of blinds seems to be found.

Our criticisms, however, must be two. In the first place, these writers are assuming, again, not true conditioning, but sign learning. The positive response of going down

* For a further elaboration of this type of criticism, see Williams⁽⁸¹⁾ and Chapter XXI of the book by Tolman.⁽⁶⁷⁾

† See references 22, 23, 24, 25, and 26 in the bibliography.

a true path segment can hardly be said to be the same response as that made to the final food—the latter is eating, the former that of entering and traversing. It can hardly be said, therefore, that the positive response to the food, as such, becomes conditioned to the true path segments. The response to an alley segment is a response to the latter as a sign for the to-be-reached food. Our second criticism is that the goal gradient hypothesis itself seems hardly a true conditioned reflex principle. If true, it seems to argue not for a conditioned reflex theory, but for a field theory. How can responses nearer the goal be conditioned more strongly than those farther away unless the rat has already come in some sense to be sensitive to the field relationship of being nearer to the goal?

It may be noted, finally, that Guthrie ⁽¹³⁾ has attempted to add further support to the conditioned reflex doctrine by suggesting that many of the important connecting links in the process of conditioning may be internal postural and proprioceptive responses and stimuli: that these fill in and eke out the connections between the external stimuli and the external responses. Still more recently, ⁽¹⁴⁾ however, even he has admitted that theories which thus seek to explain learning by such purely hypothetical and experimentally non-attackable entities as these internal responses and internal stimuli can have but little pragmatic value for present-day psychology.

Let us turn now to the conditioned reflex theories and the higher forms of learning.

4. The conditioned reflex theories and the higher forms of learning.—The conditioned reflex theories attempt, in general, to explain the higher forms of learning by assuming *symbolic* responses and the conditioning of these responses. Such symbolic responses are conceived as some sort of internal affair. They do not exhibit themselves overtly. They become conditioned to external stimuli and result in internal stimuli, to which external responses may in their

turn be conditioned. This notion of symbolic responses obviously takes as its model the facts of internal speech in human beings. But chimpanzees, dogs, and even rats (in some measure) are capable of the higher forms of learning, and yet they obviously do not have internal speech. It seems, therefore, now to be assumed by the conditioned reflex theorists, especially by Hunter,* that these animals must be capable of some more primitive sort of internal symbolic process. Thus, Hunter defines a symbol as "any process which is a substitute, which can arouse a selective response, and which can be recalled if it ceases to be present."^(28:67) And he assumes that the lower animals, in so far as they are capable of delayed reaction, double alternation, insight, and reasoning, must have ascribed to them some primitive form of such symbolic processes.†

Finally, however, the present writer would assert that whether such higher forms of learning do or do not require the assumption of symbolic responses, they most certainly do imply something more than mere conditioned reflex principles. Far more than the simple facts of conditioned reflexes or of trial and error, the higher forms of learning point to the need of field principles. But more of this later.

Let us turn to the trial-and-error theories.

* See references 28, 29, 30, 31, 32, 33, and 34 in the bibliography.

† In this general connection it may be noted that Maier,⁽⁵⁵⁾ in investigating the effects of cortical destruction upon the ability of his rats to "reason," seemed to find something like an "all or none" principle. He found that a relatively small destruction of the cortex (18 per cent) destroyed the ability to "reason" completely, whereas destructions up to that amount did not injure it appreciably. Lashley,⁽⁴⁸⁾ on the other hand, for ordinary maze learning (trial-and-error learning) found no such sharp division, but merely a very gradual decrease in ability with increasing amounts of destruction. This difference between the two findings lends some support, perhaps, to the notion that "reasoning" requires a unique sort of function (that is, symbolic processes).

Reflex-Arc Theories—Trial-and-Error Theories

It is Thorndike ^(62, 63, 64) who has most clearly enunciated a trial-and-error theory, and the following discussion will be limited, for the most part, to a consideration of the earlier and later forms of his theory. We shall begin with a consideration of his theory in relation to the trial-and-error facts themselves, and then return to it in connection with conditioned reflex learning, sign learning, and the higher forms of learning.

1. **Trial-and-error theories and the trial-and-error facts.**—The facts of trial-and-error learning, as conceived by Thorndike, may be schematized as follows:

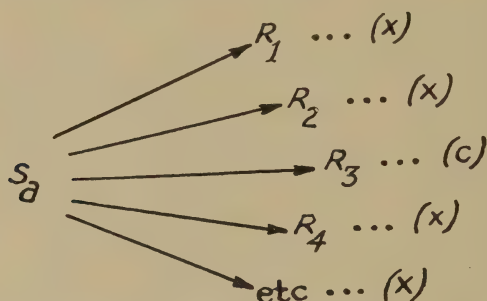


Fig. 62.—Schematization of Trial and Error Learning.

R_1 , R_2 , R_3 , R_4 , and so on, represent an original array of alternative responses—trials and errors—called out, innately or as a result of previous learning, by the one stimulus situation S_a . The x 's after R_1 , R_2 , R_4 , and so on, indicate that these particular R 's prove incorrect responses, whereas the c after R_3 indicates that this one proves the correct response. Thus, learning is said to consist in the relative strengthening of the one "connection" S_a-R_3 and the relative weakening of the other "connections" S_a-R_1 , S_a-R_2 , S_a-R_4 , and so on.

The theory, as initially formulated by Thorndike,* emphasized two main laws to explain such strengthenings and weakenings. He called them the "Law of Exercise" and the "Law of Effect." According to the "Law of Exercise," the one connection S_a-R_3 tends to become relatively strong in comparison with the other alternative connections in so far as this correct connection receives more "frequent" (or recent) exercise than do the other connections. And according to the "Law of Effect," this one connection S_a-R_3 also tends to become relatively strong in so far as it is followed by a "satisfier" or in so far as the other alternative connections are followed by "annoyers."

We must now consider these two laws in more detail.

The "Law of Exercise." This law has been widely accepted. Of late, however, there have been a number of attacks upon it—including one by Thorndike himself. But in order to understand the pros and cons of these attacks, we must first note that there are really several possible meanings or points of application for this concept of exercise, and that these are often confused. Altogether, there seem to be four such meanings or points of application, as follows:

(1) Exercise of R_3 at the expense of the other, initially alternative R 's. This is the meaning specifically stated in Thorndike's original doctrine.⁽⁶²⁾

(2) Continuation of exercise, that is, "overexercise" of R_3 after the tendencies to the other alternative R 's have dropped out. This would be a new meaning not, as such, mentioned in the original formulation.

(3) Exercise in the mere presentation of a sequence of two stimuli, for example, S_a-S_b , to each of which, as in Figure 63, it is assumed that a response is already attached. This, again, is a new meaning not specifically stated in the original formulation.

(4) Exercise on one total trial-and-error stimulus situation, such as S_a , as compared with exercise on another total

* See reference 62 and Vol. II of reference 63 in the bibliography.

trial-and-error stimulus situation, such as S_b , as illustrated in Figure 64. Here the notion would be that the one stimu-

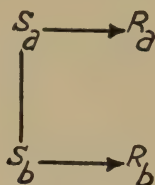


Fig. 63.—Schematization of the Exercise of the Sequence of Two Stimuli, Each Connected with its Own Response.

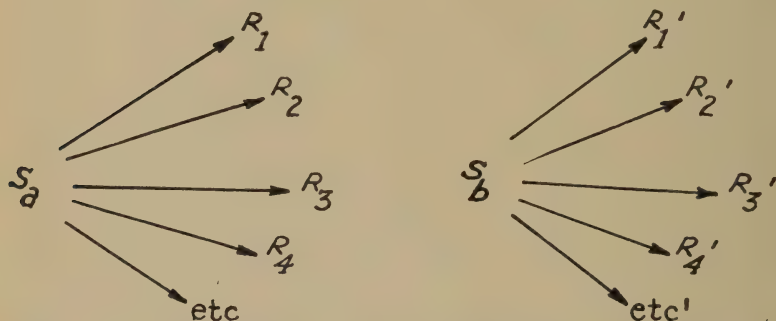


Fig. 64.—Schematization of Two Independent Trial-and-Error Situations, in One of Which the Frequency of Exercise May Be Made to Exceed That of the Other.

lus situation receiving the greater total exercise would be more likely thereafter to evoke its appropriate response. This also is a new meaning not stated explicitly in the original theory.

We must now consider the experimental findings relative to each of these four meanings of exercise.

(1) *Exercise of R_s at the expense of the other, initially alternative R 's.* The recent attack upon the "Law of Exercise" has concerned itself primarily with disproving the law's efficacy in this specific sense.

Studies under Carr's direction, at Chicago,* with both

*See, for example, references 1, 36, 53, 71, and 75 in the bibliography.

rats and human beings have shown that being forced by blocks or other devices to take the true path more frequently than the blinds does not in and of itself induce any clearly and uniformly greater propensity for taking the true path. Or, as Carr sums it up, it appears that "... a certain number of errors must be made, that is, a certain amount of exercise on the wrong path must be allowed, and eliminated before the subject is ever able to run the maze correctly. Correct modes of response are established in part by learning what not to do." (6:98)

Again, a number of other experiments indicate that in the ordinary trial-and-error set-up, the animal usually starts with no advantage of frequency and recency of exercise of the correct response—that greater frequency results from learning, and not vice versa. In particular, Kuo's experiment⁽⁴⁷⁾ with a four-door, multiple choice box indicated that all four doors were chosen with approximately equal frequency until after learning set in; and then they were eliminated only in terms of the order of undesirability of their respective results.

Finally, perhaps the most striking disproof is Thorndike's own,* obtained in a series of recent experiments. He used human subjects. In one typical experiment, he required the subjects to try repeatedly to draw a line four inches long without being able to see their results. Some lengths were initially drawn more frequently than others, but there was no tendency for these lengths to become still more frequent as practice continued. Mere initial frequency as such showed no tendency in and of itself to stamp in a response.†

* See Chapter II of reference 64 in the bibliography.

† Recently Elliott⁽¹⁰⁾ has performed a somewhat similar experiment with rats. He used a multiple choice box consisting of five alleys leading from the large end of a wedge-shaped compartment. The animal was allowed to choose only one of the five alleys, and he obtained food regardless of which one he chose. A group of rats that were not very hungry, and to which the finding of the food was no great reward, con-

Finally, as further support for the disproof of exercise in this first sense, we have Dunlap's Beta hypotheses.^(7, 8) Dunlap found that the best way to eradicate any undesired response was actually to exercise this incorrect response (but with emphasis upon its incorrectness).*

(2) *Continuation of exercise, that is, "overexercise" after the other tendencies have dropped out.* Although it seems from the above that greater frequency (or recency) of the one response at the expense of the other alternative responses does not cause the one to be selected, this fact does not necessarily mean that further exercise upon that one response *after* it has been selected will have no effect. Indeed, it now appears from some recent experiments that "overexercise" upon R_3 after the tendencies to the other competing R 's have disappeared does cause a special sort of "fixation."

Gilhausen⁽¹²⁾ found that rats which had been overtrained in the taking of a more difficult path—one made of jumps—would persist in this jumping path for an unduly long time even when another much easier, continuous path was offered alongside of the jumps. And Krechevsky and Honzik⁽⁴⁶⁾ have shown that if rats are overtrained to take the shorter of two alternative paths to food, they will persist unduly in choosing this first path even after the situation has been changed so that the path which was originally shorter has become the longer. Further, they found the degree of this persistence or "fixation" to be

tinued to vary among all five paths. The initial frequencies, such as they were, did not determine any final stamping in. This was similar to Thorndike's finding. With another group of rats, which, on the other hand, were very hungry, a very strong frequency on some alley developed right from the beginning—but this was always one of the side alleys, and there was no evidence of a *gradual* heaping up on these alleys. Once they were tried, they were adhered to quite uniformly.

*For a more extended review of all the arguments against the "Law of Exercise" in this sense, see Chapter XXII of Tolman's book.⁽⁶⁷⁾ In particular, Peterson^(57, 58, 59) has presented important evidence against it, with human subjects.

approximately proportional to the amount of the original "overexercise."

It must be concluded that even though an initial excess frequency on one path at the expense of other alternative paths is not the cause of the initial selection of the one, still a continued overexercise of this one *after it has been selected* will cause it to become excessively stamped in, or "fixated." *

(3) *Exercise of a sequence of two stimuli.* Here we refer again to some of Thorndike's recent experiments.† Thorndike presented pairs of verbal stimuli to human subjects, and found that a pair of such stimuli do not become associated merely as a result of frequent presentation—that is, merely as a result of exercise—unless the two items possess, or can be made to possess, for the subjects in question, a property of "belonging" to one another. Thus, to return to Figure 63, let S_a and S_b represent the two successive verbal stimuli, and R_a and R_b the corresponding responses of naming them. What Thorndike found was that mere frequent presentation (exercise) of the stimulus sequence S_a — S_b would not as such cause the subject later, upon being presented with S_a alone, to give R_b as well as R_a ; it was only when S_a and S_b had some property of "belonging" to one another that such repeated exercise developed this associative tendency.

(4) *Exercise in the sense of greater frequency or recency on one total stimulus situation, S_a , than on a second total stimulus situation, S_b* (see Figure 64). The validity of exercise in this sense as a conditioner of learning can hardly be questioned. If a given rat has been presented with one maze-bifurcation, S_a , 100 times, and with another maze-bifurcation, S_b , but 5 times, it is obvious that, other things being equal, he will now be more able to make the correct

* Hamilton and Ellis^(15, 16) have found that cortical destruction also tends to favor such "fixation" or, as they call it, "behavior constancy."

† See Chapters III and IV of reference 64 in the bibliography.

response at S_a than at S_b . But he will do better after the 100 trials not because these trials have given him more chances to exercise the right response "at the expense of" the wrong, but rather because they have given him more chances to try out both right and wrong responses (and hence to have been affected by the differences between the results).

To recapitulate:

1. Forced or chance exercise of the right response at the expense of the wrong responses is not the cause of the initial selection of the right response. In this sense, the "Law of Exercise" does not hold.

2. Once, however, the right response has been selected, continued repetition—that is, overexercise—of this right response (together with its good consequences) may cause this response to become "fixated." In this sense, a "Law of Exercise" does hold.

3. Exercise of a sequence of two stimuli: Mere frequency of presentation without attendant "belonging" does not cause two stimuli to become associated. In this sense, a "Law of Exercise" does not hold. (Only with attendant "belonging" does exercise here prove efficacious.)

4. Greater frequency or recency on one total stimulus situation as compared with another total stimulus situation: The more frequently (or recently) a given situation has been presented, with opportunities for both right and wrong responses, the more likely that the correct response will now be made to that stimulus situation. In this sense, a "Law of Exercise" does hold.

So much for the pros and cons as to the "Law of Exercise." We turn now to the "Law of Effect."

The "Law of Effect." Originally, Thorndike gave about equal weight to the two laws. But since, as now appears, the "Law of Exercise" in Sense 1 does not hold, he now

puts practically the entire burden for selective trial-and-error learning on his "Law of Effect."

Thorndike's original formulation of the "Law of Effect" read:

When a modifiable connection between a situation and a response is made and is accompanied or followed by a satisfying state of affairs, that connection's strength is increased: when made and accompanied or followed by an annoying state of affairs, its strength is decreased.*

And: "By a satisfying state of affairs is meant roughly one which the animal does nothing to avoid, often doing such things as attain and preserve it. By an annoying state of affairs is meant roughly one which the animal avoids or changes." †

Thorndike has discovered recently, however, that even this law does not hold in a simple form. He has found ⁽⁶⁴⁾ that annoying after-effects do not necessarily weaken in the same way that satisfying after-effects strengthen. Annoying after-effects are various in their action. They may even so "upset" the animal as to cause the latter to do the very same response over again. Satisfying after-effects, on the contrary, are always beneficial. They always lead to the strengthening of the connection that has just preceded them.

Now, it is obvious that in a loose, descriptive sense, this law does hold. Animals and men do, in the long run, come to exhibit those responses which lead to satisfying after-effects, and they do cease to use those which lead to less satisfying or to positively annoying after-effects. But the truth of this general description of the final facts does not necessarily prove the truth of the law that Thorndike assumes to explain those facts. According to the law, learning should take place only *in the degree to which the correct response is followed by satisfying effects (or the degree to*

* See Vol. II, p. 4, of reference 63 in the bibliography.

† See Vol. I, p. 123, of reference 63 in the bibliography.

which the incorrect responses are followed by annoying after-effects). But experimental work on "latent learning" contradicts this, for as far as this type of learning is concerned, the rats "learn" just as fast with but little if any reward. This learning does not appear in their performance until after a good effect has been introduced, but it takes place none the less. We must, in short, distinguish as does Elliott ⁽⁹⁾ between "learning" and "performance." The "latent learners" do not, during the nonreward period, perform in correspondence with their learning. Only after the reward has been introduced does their performance come up to their learning. We are forced to conclude that while the "Law of Effect" may hold descriptively for "performance," it does not hold for learning *per se*, or at any rate, that it does not hold for the latter in the same degree. An animal in trial-and-error learning is not "stamping in" one *S—R* connection and "stamping out" other alternative *S—R* connections. Food and lack of food, shock and lack of shock, blind end and open path, the word *right* and the word *wrong*—these do not stamp in or stamp out; they result. And the animal learns simply, on a basis of exercise (in Sense 3 of the meanings above) and on that of "belongingness," these good and bad (or, it may be, merely neutral) results.*

* Relative to a general discussion of the "Law of Effect," several points are to be added. Thorndike, as we have seen, calls the effects "satisfiers" and "annoyers," and originally ⁽⁶²⁾ attempted to give them a physiological explanation in terms of increased and decreased "conductivity of nerve paths."

Hobhouse, ⁽¹⁸⁾ on the other hand, describes these effects as confirmation and inhibition. Holmes ⁽¹⁹⁾ thinks of them as congruity and incongruity, with some total instinctive activity. And Carr ⁽⁶⁾ has defined them as increased and decreased consequences in the way of resultant sensory intensities.

Finally, Watson ⁽⁷⁶⁾ in his *Comparative Psychology* denied the "Law of Effect" altogether and adhered to the "Law of Exercise" (in its now disproved meaning, Sense 1 above).

Further, it is to be pointed out that even though learning be not a matter of good effects stamping in but rather, as we would here contend,

We turn, now, to Thorndike's theory as applied to the other three types of learning fact.

2. The trial-and-error theory and conditioned reflex learning.—The trial-and-error theory originated before there was any widespread knowledge of the conditioned reflex facts. Some of the original adherents of a trial-and-error theory have, therefore, now gone over to the conditioned reflex type of theory.* But Thorndike still adheres to the trial-and-error doctrine. He suggests that the conditioned reflex may either be the same as what he earlier called "associative shifting," or may be a specialized sort of learning characteristic of physiological reflexes only. "Associative shifting" was a concept presented by Thorndike in 1913.† It is really much the same phenomenon as that we have called "sign learning." We turn to it now, therefore, under the next caption.

3. The trial-and-error theory and sign learning (that is, associative shifting.)—Associative shifting, as Thorndike defines it, is the fact that if a response is already attached to one stimulus element or set of stimulus elements, this response can be shifted to other stimulus elements that are presented in conjunction with the first element or set of elements. He writes:

[One holds up] before a cat a bit of fish, saying, "Stand up." The cat, if hungry enough, and not of fixed contrary habit, will stand up in response to the fish. The response, however, contracts bonds also with the total situation, and hence to the human being in that position giving the signal. . . . After enough trials, by proper arrangement, the fish can be omitted, the other elements of the situation serving to evoke the response. Association may later be further shifted to the oral signal

a matter of discovering and retaining "what leads to what," it may still be true that if the final "whats" are relatively good (nondisruptive), this fact may have a favorable influence on retention. Boring recently⁽⁵⁾ seems to have suggested some such interpretation.

For further discussion of the "Law of Effect," see Chapter XXII of Tolman's book,⁽⁶⁷⁾ Tolman, Bretnall, and Hall,⁽⁶⁸⁾ and Tolman.⁽⁶⁸⁾

* See, for example, Watson.⁽⁷⁷⁾

† See Vol. II of reference 63 in the bibliography.

alone. With certain limitations due to the necessity of getting an element of a situation attended to, a response to the total situation A B C D E may thus be shifted to B C D E to C D E, or to D E, to E. Moreover, by adding to the situation new elements, F, G, H, etc., we may, subject to similar limitations, get *any response of which a learner is capable associated with any situation to which he is sensitive.**

This situation reduces to sign learning. That is, the frequent presentations of the stimulus combination S_a-S_b cause a preparatory response to become attached to S_a . (S_a has become a sign for S_b .) "Stand up" has become a sign for "fish," and the cat behaves toward it as such.

4. The trial-and-error theory and the higher forms of learning.—No clear statement is here forthcoming. Thorndike says little about the problem save to assert that he could discover no evidence for such higher forms in cats and dogs.⁽⁶²⁾† Watson explained all the higher forms as dependent upon internal speech, and then, since the lower animals can be assumed to have no such speech, he denied that they exhibit higher learning.⁽⁷⁶⁾ Yerkes^(83, 84) adopts a dualistic position, and postulates that when sudden drops occur in an otherwise gradual trial-and-error sort of curve, there is operative a truly mental sort of entity, which he calls "insight" or "foresight" or "getting the idea."‡

We are ready now to consider the field theories.

Field Theories

The field theories, taken as a group, may be said to agree on the following assertions: (a) An animal responds always to a whole field of environmental stimuli and never to a single isolated stimulus. (b) The result in the animal of such a whole field of stimuli is an organized—Gestalt—

* See Vol. II, p. 15, of reference 63 in the bibliography.

† Adams,⁽²⁾ however, has since repeated Thorndike's experiment and finds evidence for such higher forms of learning in the very same sorts of situation.

‡ For a helpful analysis in this connection, see Hunter.⁽²⁷⁾

adjustment. (c) This organized or Gestalted adjustment need not lead to any overt behavior during that situation.* (d) Learning consists in some sort of a reorganization, or regestalting, of this adjustment, and "dynamical" principles rather than associationistic ones play the major rôle in such reorganizations. (e) Such reorganizations come from the impetus of a need or needs, together with some obstruction to any immediate, already-acquired, easy route to the satisfaction of such need or needs.

The different subvarieties of the field theories would differ only in their respective emphases upon these various points. Lashley^(48, 49, 50) emphasizes the nonlocalized character of the cortical basis for such adjustments. Wheeler^(79, 80) asserts the first importance of a law of least action. Köhler^(39, 40) and Koffka^(37, 38) emphasize the perceptual, Gestalt character of the adjustment and a phenomenon of "insight" as involved in its reorganization. Adams,⁽¹⁾ following Lewin,⁽⁵¹⁾ asserts that the adjustments may themselves be depicted as "fields," and emphasizes the importance of needs and obstructions in inducing the reorganizations in such "fields." Tolman⁽⁶⁷⁾ emphasizes the

* That behavior of some sort even though not overt is necessary in learning appears now from the recent, extraordinarily important experiments of Harlow and Stagner,⁽¹⁷⁾ who have shown that cats and dogs cannot acquire conditioned skeletal avoidance responses when under the influence of the drug curare. This drug paralyzes the striate musculature by acting upon the myoneural junction to prevent the passage of nerve impulses from the motor neurone to the muscle fibre. When cats or dogs are under the influence of this drug, if a bell and light be presented just before an electric shock (to which latter they can make no response because of their paralyzed condition), they acquire no conditioning. That is, after they come out of the curare, they make no avoidance to the bell and light without further training.

The dilation of the pupil which occurs under the curare does, however, become conditioned to the bell and light.

If the field theories are to survive, they must allow for these facts. They must admit that actual responses are thus in some sense and in some degree necessary for learning, even though, as they would maintain, such responses are not necessarily gross, overt, and entirely carried through.

behavioristic character of the adjustments in the sense that their functional significance is to prepare the animal for behavior, and he lays special stress on the fact that the reorganizations which constitute learning involve "sign-gestalts" within the larger "fields." But let us amplify.

Lashley,^(48, 49, 50) as a result of his experiments upon the effect of cortical destruction upon learning and retention in rats and monkeys, has abandoned reflex-arc hypotheses. He has demonstrated that, within wide limits, it is not the locations but the amounts of cortical destruction that are important. Learning, from his point of view, is carried in the form of neural patterns that somehow preserve their identity in spite of variations among the sensory, the cortical, and the motor elements. When a rat has learned a maze, he has acquired something that he retains despite the possibility of wide changes among his momentary visual, tactual, and kinæsthetic stimuli.*

Lashley writes:

I believe that for every reaction, above the level of a spinal reflex, the adequate stimulus is a pattern which is effective when applied anywhere upon the sensory surface, and the motor response involves an equally variable grouping of motor neurones. . . . We have seen that the adequate stimulus in such cases [habits based on vision, kinesthesia, and touch] is not the specific cells activated, but the pattern of excitation which may shift over the sensory surface and likewise over the cortical field. In such a pattern the relative intensity, distance of separation, and frequency of excitations seem to be the only constant factors.^(50:245) †

Wheeler⁽⁷⁹⁾ and Wheeler and Perkins⁽⁸⁰⁾ assert that

* See, in this connection, some recent experiments by Tryon⁽⁷⁰⁾ and by Honzik,⁽²¹⁾ in which after the maze was learned, "short cuts" were introduced without upsetting the animal's performance, and also the experiments by Macfarlane,⁽⁵⁴⁾ in which the rats changed from swimming to wading and vice versa without upsetting what they had learned.

† See also the *supremely important* recent experiments and argument of Klüver⁽³⁵⁾ relative to what he calls the "equivalence of stimuli" (in monkeys).

learners are energy systems; that goals establish stress differentials in the nervous system; that when these stresses exist, there will be action from high to low potentials until such differentials are resolved; and that learning is the result of the resolution of these stress differentials. They emphasize the dominance of a "Law of Least Action" in such resolutions.*

Köhler^(39, 40) and Koffka^(37, 38) assume that learning is equivalent to a perceptual reorganization in which dynamical principles rather than the stamping in or out of associations play the major rôle. In particular, they emphasize the phenomenon of "insight." Koffka writes:

The sudden grasping of the solution which results is a process that runs its course in accordance with the nature of the situation, so that the complete solution of the problem takes place with reference to the configuration of the field of perception; and this is what Köhler maintains to be the criterion of insight.^(37:214) . . . Even Thorndike's experiments seem to show, not only that the animal experiences certain vague total situations, but that, in the course of learning, this total situation becomes organized. When the loop differentiates itself, it is not as if it were now seen as a circular or elliptical figure of definite magnitude and color; it is merely "something to be struck at," or "something to be moved." As such, it becomes the central feature in the total phenomenal situation.^(38:190)

Adams,⁽¹⁾ influenced by Lewin,⁽⁵¹⁾ † indicates that the organized adjustments that intervene between stimulus-field and response are themselves describable as "fields." Given the organism's "sensitivities," "retentivities," and "needs," a given stimulus-field will give rise in the given organism to an adjustment that is a psychobiologically modified "image" of the actual stimulus-field. Lewin and Adams have called this the "psychobiological field." Such a psychobiological

*For a helpful analysis of the Wheeler and Perkins doctrine, see McGeoch.⁽⁵⁶⁾

† Bellows⁽⁴⁾ in a recent article seems to adopt much the same position as that of Adams.

field * is to be conceived as constituted by all the stimulus-objects that, on the given occasion, are in the organism's actual physical, social, and ideational environments (*in the manner and in so far as the organism is sensitive to these environments*), plus the "direction" and "distance" relations of these objects one to another and to the organism (in so far as it is also sensitive to such direction and distance relations), plus the fact of his positive and negative "demands" for and against such objects. The psychobiological field is thus the environmental *milieu* (*such as it is for the organism*) at the center of which the latter finds itself and relative to which it behaves. This *milieu* seems, as regards the behavior of the organism, to radiate from it as a center, the objects along its radii being in varying degrees demanded-for or demanded-against (that is, loaded with positive or negative "valences"). The objects which thus have valences may be "get-at-able" by relatively direct routes, or they may be barred off by "barriers" or "obstructions." Learning, according to Adams,⁽¹⁾ is a remaking of such a psychobiological field under the stress of the need for a valenced object, plus the factor of some initial barrier or obstruction between the organism and the valenced goal-object.†

In the remaining pages of this chapter, there will be attempted a somewhat more extended account of the present writer's variety of the field theory. The present writer starts from the doctrine of Adams and Lewin, but asserts

* The present writer has elsewhere suggested the phrase "means-end-field" to designate this concept. See Chapters VI to XI of reference 67, and reference 66, in the bibliography.

† These concepts of a "psychobiological field," that is, of "direction," "distance," "barriers," "valences," and so forth, are used, of course, purely symbolically. They are used as a symbolic medium in terms of which to represent the situation for the organism not only when the stimulus-field itself is an actual spatio-physical one, but even when the latter is, say, a temporal or a social one.

that, for the problem of learning, the important relations in the "psychobiological fields" are "sign relations." "Learning" he would describe as the new formation, or the reformation, of "sign-gestalts" within the larger psychobiological fields. The theory is therefore to be designated a "sign-gestalt" theory.

Sign-gestalts are to be conceived as having three parts: a *sign*, a *significate*, and a *behavior-route leading from sign to significate*. A sign-gestalt is equivalent to an "expectation" by the animal that "this," (that is, the sign) "if behaved to in such and such a way" (that is, the behavior-route), will lead to "that" (that is, the significate). A sign-gestalt sets the animal to "expect" that when he actually behaves, "this" field-feature will lead, "by such and such a behavior-route," to "that" field-feature. And learning, according to the theory, will consist in the making or the remaking of such expectation-sets under the hard tutelage of the outcomes experienced as the result of the actual behaviors that are tried.

We may now consider this doctrine with respect to each of the four types of learning fact.

1. The sign-gestalt theory and conditioned reflexes.—The sign-gestalt theory asserts that the conditioning of a reflex is the formation of a new sign-gestalt. It asserts that a conditioned reflex, when learned, is an acquired expectation-set on the part of the animal that the feature of the field corresponding to the conditioned stimulus will lead, *if the animal but waits*, to the feature of the field corresponding to the unconditioned stimulus.* Several facts seem to support this interpretation.

First, there is the fact of "experimental extinction." The conditions of experimental extinction indicate that if it be

* But an animal will not learn such a sign relation, as the Harlow and Stagner experiment ⁽¹⁷⁾ indicates (see the footnote on page 389), unless the animal be able to make some degree of appropriate response to the unconditioned stimulus and perhaps also to the conditioned stimulus.

proved to the animal that the conditioned stimulus will no longer be followed by the unconditioned stimulus, the conditioned reflex will disappear. In other words, the normal continuance of a conditioned reflex is equivalent to an "expectation" on the part of the animal that the field-feature corresponding to the unconditioned stimulus is going to follow, and, if this expectation fails to be verified, the conditioned reflex will disappear.

Delayed and trace reflexes are also in point. In other words, when there is an appreciable interval of time between the beginning of the conditioned stimulus and the beginning of the unconditioned stimulus, the reflex tends to delay its appearance until about the appropriate time for the coming of the unconditioned stimulus. But this fact indicates, further, that in the holding off of the conditioned reflex there is involved something equivalent to an assertion by the animal as to how long he must wait after the field-feature corresponding to the conditioned stimulus for the coming of that corresponding to the unconditioned stimulus.*

* The other distinctive features of conditioned reflexes such as, for example, positive and negative induction, while not such an inevitable part of a sign-gestalt doctrine, do not, it would appear, conflict with the latter. Positive and negative induction are phenomena that arise when the animal is made to differentiate between two closely similar stimuli. When this is the case, it is forced to learn that one of these stimuli is truly the sign for the unconditioned stimulus whereas the other is not. Positive induction then appears in the further fact that if now the non-sign stimulus be presented just prior to the sign stimulus, a bigger positive reaction to the latter is obtained. The fact of negative induction is just the reverse. If the sign stimulus be presented just prior to the non-sign stimulus, the lack of response to the latter is reinforced. But this means that when the two stimuli are experienced in close juxtaposition, the sign stimulus, by contrast, reinforces the non-sign stimulus, and vice versa. This is an interesting and perhaps surprising fact—but not one that contradicts the sign-gestalt theory.

The further feature of "irradiation" is not so easy to fit in. But considerable doubt has recently been cast on the supposed basic facts underlying the concept of irradiation (see Loucks ⁽⁵²⁾).

What, it may be asked, distinguishes the conditioned reflex, according to this sign-gestalt theory, from other types of learning? The answer is that in the conditioned reflex, the only obvious response that seems to be made to the sign is a beginning of the response that will normally be made to the significate after the latter arrives. But this means, to put it another way, that in conditioned reflexes, the relationship between the unconditioned stimulus and the conditioned stimulus is primarily one of but mere *temporal* sequence. Hence, the only behavior with which the animal will respond to the field-feature evoked by the conditioned stimulus, after he has learned the sign relationship, is that of merely *waiting* and then beginning on the original unconditioned response at about the time appropriate for the appearance of the field-feature corresponding to the unconditioned stimulus.

Finally, what, according to the sign-gestalt theory, would be the laws of the conditioned reflex? We suggest two: (a) a "Law of Belongingness" and (b) a "Law of Exercise."

a. The "Law of Belongingness" would state that conditioned reflexes become established only when the experimental set-up is such as to make the field-features corresponding to the two stimuli stand out from a common background, that is, to "belong" together, to stand out as a "figure on a ground." This law is testified to by the great emphasis that has to be put experimentally upon ruling out all distracting field-features. It is distinctly a "dynamical," gestaltish, sort of law.*

b. The "Law of Exercise" would be understood in Sense 3 (see above, page 379). It would state that, given such "belongingness," the strength of a conditioned reflex will at any given time be relatively proportional to the frequency and

* The fact that Thorndike himself has now had to help himself out with such a law means, we would say, that his trial-and-error "connectionism" has really failed him.

recency with which the sequence of the two stimuli—the conditioned and the unconditioned—has been presented.*

And, finally, there would be some “Law of Response” (derived from the Harlow and Stagner experiment) to the effect that an unconditioned stimulus does not evoke a field-feature unless it is in some degree responded to.

Let us consider now the sign-gestalt theory with respect to sign learning.

2. The sign-gestalt theory and sign learning.—It is obvious by now that what the sign-gestalt theory does is to reduce all learning to the pattern of sign learning. Sign learning is taken as the prototype for all learning. In sign learning, one field-feature becomes the sign for another field-feature, and the response that appears as a result is appropriate to the temporal and other characteristics of this sign relationship. Such a description has just been shown to hold for the conditioned reflex. And, obviously, it holds for the cases that we have specifically labelled sign learning: the dog’s response to the sound of my approaching automobile, the “flutter” response of Wever’s cat, and the gentle dropping-off response of Warner’s rats.

In the next two sections, we shall try to show that such a description likewise holds for trial-and-error learning and for the higher forms of learning.

3. The sign gestalt theory and trial and error.—Trial-and-error learning consists, according to this theory, in learning “what” each of the initially alternative responses “leads to.” Thus, given the situation shown in Figure 65, the theory says that what the animal learns is that the initial field situation F_a , responded to by the response R_1 , will lead to the resultant field-feature f_1 ; responded to by R_2 , will lead to the field-feature f_2 ; etc. The result of its learning is, thus, that F_a becomes the sign for all the different alternative significates f_1, f_2, f_3 , and so on. Or, in other

* For a more extended discussion of a sign-gestalt interpretation of the conditioned reflex, see Chapter XXI of Tolman’s book.⁽⁶⁷⁾

words, it learns the whole array of alternative sign-gestalts, $F_a-R_1-f_1$, $F_a-R_2-f_2$, and so on.* But the animal's final

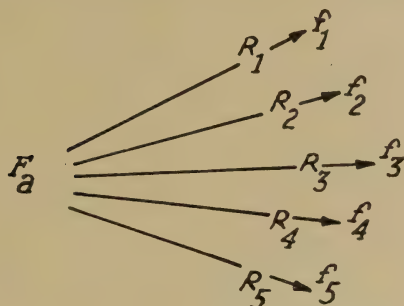


Fig. 65.—Schematization of Trial-and-Error Learning in Terms of the Sign-Gestalt Theory.

taking of R_3 (the correct response) rather than any of the others is something not part of this learning *per se*. It indicates the further fact that under the motivation conditions of the moment, the one sign-gestalt f_3 is more demanded by the animal than are any of the other alternative sign-gestalts f_1 , f_2 , f_4 , and so on. (See the discussion above, page 386, of "latent learning.") †

* In this figure for the sign-gestalt theory, we have used F_a , f_1 , f_2 , f_3 , and so on, rather than S_a , s_1 , s_2 , s_3 , and so on, in order to emphasize the fact that according to the sign-gestalt theory it is the psychobiological field-features resulting from the stimulus situations rather than the latter themselves that are combined into sign-gestalt wholes. In the previous presentation of the sign-gestalt theory,⁽⁶⁷⁾ O's instead of F's and f's were used to symbolize these field-features, that is, signs and sign-gestalts that enter into a sign-gestalt.

† It is to be noted also that, as appears from some recent experiments by Krechewsky (see references 41, 42, 43, 44, and 45 in the bibliography), trial-and-error learning probably occurs by a succession of "hypotheses." Thus, rats, in learning a four-unit light-dark discrimination-box, were found to behave as if controlled by a succession of "hypotheses." First, an individual would choose with great consistency, say the left-hand doors; then he might change and choose perhaps alternate right and left doors consistently; and only finally would he hit upon the correct "hypothesis" of choosing all the lighted doors. Different individual rats went through different sequences of such "hypotheses." Furthermore, the order in which

What are the laws of trial-and-error learning? We suggest the following:

"Laws of Exercise." There would be laws of exercise in Senses 3, 2, and 4 (see above, page 379). We may elaborate as to each of these.

Sense 3: The theory would suppose that exercise on each trial (or error) would help to stamp in the corresponding sign-gestalt $F_a-R_1-f_1$, or $F_a-R_2-f_2$, or $F_a-R_3-f_3$, and so on. (Figure 65.) Exercise, in this sense, would help the animal to build up each of his alternative expectations.

Sense 2: The theory would suppose, further, that continued overexercises of one of these responses would tend to produce a "fixation" of it. That is, if f_3 were originally the most demanded of the alternative significates (Figure 65), then what we know about the phenomenon of "fixation" (see above, page 382) would suggest that if the animal were overexercised on the corresponding response R_3 , he would develop a relatively persistent tendency to continue with this response even if f_3 were changed so as to become relatively bad.

Sense 4: The theory would also suppose that the more frequently and recently one whole trial-and-error choice point is presented, with chances for the animal to learn all the alternative sign-gestalts, the better that choice point will be known as compared with some other total choice point presented with less total frequency and recency.

A *"Law of Belongingness."* The theory would assume that the "Law of Belongingness" would apply to the learning of each alternative sign-gestalt. Thus, the more completely F_a , R_1 , and f_1 "belonged" together, the easier would

these animals hit upon the different types of "hypotheses" seems determined in part by heredity, for it was found that Tryon's strain of maze-bright rats (see Chapter XIII) hit almost invariably upon "spatial" (that is, right, left, alternate right-left, and so on) "hypotheses" first, whereas his maze-dull strain hit upon "visual" (that is, light or dark) "hypotheses" first. This means that the sign-gestalt expectations are initiated in part by the animal himself and are "tentative."

the sign-gestalt $F_a-R_1-f_1$ be learned, and the same relation would be found in the case of the other alternative sign-gestalts.

"Dynamical" laws. The theory would assume that there must also be dynamical Gestalt laws (yet to be worked out) whereby there would be certain sorts of mutual favoring and hindering among the learning of all the alternatives: $F_a-R_1-f_1$, $F_a-R_2-f_2$, and $F_a-R_3-f_3$, and so on.

A *"Law of Motivation."* The theory would assume, lastly, a "Law of Motivation." If some one of the resultant f 's (see Figure 65) should be especially satisfying, the learning of that particular sign-gestalt, or even of the whole set of alternative sign-gestalts, would probably thereby be facilitated.*

Finally, let us consider the sign-gestalt theory in relation to the higher forms of learning.

4. The sign-gestalt theory and the higher forms of learning.—The higher forms of learning were classed, at the beginning of this chapter, as cases in which the final correct response is controlled, at least in part, by temporally absent or by unique, previously unreacted-to features of the field. It now further appears, however, that we must really distinguish between two subclasses. First, there are the delayed reaction type of problem and the double alternation type. In such problems, the situation is primarily one of *temporal absence*. And, secondly, there are the "reasoning"

* The facts of "latent learning" militate, however, against putting too great weight upon such a law. For "latent learning," as we saw above, seems to indicate that learning (though not performance) will be just about as rapid without strong selective motivation as with it. In other words, the specific character of the goals in the field may not be of overweening importance. At least, the learning under one set of mild valences (those operative during "latent learning") will carry over, without loss, to performance under a different and much stronger set of valences. The sign-gestalt theory would not, in short, put quite as much weight on specific valences and specific obstructions as Adams' theory ⁽¹⁾ would seem to do. See also Chapter XXIII of Tolman's book ⁽⁶⁷⁾ and reference 68 in the bibliography.

and "insight" sorts of experiment, in which the situation is both one of temporal absence and one where an important controlling feature has not, *as such*, been experienced as a result of the given behavior but has to be "inferred." Let us consider each of these types separately.

Temporal absence. In the delayed reaction problem, the animal, after having learned that an actually lighted door leads to food, is required to learn further that a door which has just been lighted leads to food. And in the double alternation problem, the animal, after having learned that both paths lead, spatially, back to food, must learn further that, though the first round trip to, say, the left is a sign for the same path's being open again, the second round trip to the same side is a sign for the opposite path's being open. Hence, his sign for a correct third round trip must include not only the field-features involved in the immediately preceding second round trip but also those of the still earlier first round trip. In both delayed reaction and double alternation, the essence of the ability to perform the correct moves seems to consist in the animal's being able to build up a sign-gestalt in which an essential feature or element of the total sign is temporally absent at the moment of behaving. In the delayed reaction-box, the light, which constitutes a large part of the sign governing the correct response, that is, the correct sign-gestalt expectation, is already past. And in the double alternation box, a large part of the sign governing a correct third trial is the field-features involved in the first trial—and these also are, at the moment of behaving, decidedly past.

Temporal absence plus creative inference. In the Maier reasoning experiments, the rat,⁽⁵⁵⁾ after having learned all three table-tops and their interrelations, is placed on one table and finds a bit of food on it. Then the animal is carried to one of the other two tables, where it has to respond by going to the table upon which it has just been fed, rather than to one of its other two alternatives. To do this re-

quires, however, a sign-gestalt in which the immediately preceding feeding on the now distant table and the present relations to that distant table are combined into one sign. And on the basis of this sign, the rat must expect a resultant significate of food on that now distant table. But the production of this expectation involves something more. In its preceding training, the rat has not found food on any of the tables. That is, it must now, as it is starting to run, use an experience of the immediate past in a distant part of the field as a sign *creatively* to infer a significate that it has never, as such, specifically experienced as resulting from the behavior with which it must now respond.

The Tolman and Honzik insight experiment ^(67:167) presents a similar situation. After having experienced the block in Path 1, the rat must creatively infer it in Path 2. It must creatively build up a sign-gestalt with this temporally past experience (a block in Path 1) in one part of the field as part of the sign so that it shall expect a significate (a block in Path 2) to result from the behavior of running down Path 2—although it has never before experienced such a result from this Path 2 behavior.

But what, finally, are the new laws, if any, involved in such higher forms of learning? We do not know. We can merely say that these higher forms certainly involve all the laws of mere trial-and-error learning plus some new ones. And the new laws, whatever they may eventually prove to be, will be concerned with the ability to build up sign-gestalts that, on the one hand, include in the sign field-features that are temporally past and, on the other hand, include in the significate field-features that are creatively inferred.

Are symbolic processes necessary for building up these sign-gestalts? This is a question that we shall not here attempt to answer. We human beings know from our own experience that such symbolic processes would undoubtedly be helpful. But whether the logic of the situation abso-

lutely requires them, the sign-gestalt theory will not at present attempt to say.

Summary

In conclusion, a brief summary may be helpful: (1) The facts of animal learning are to be classed under four rubrics: conditioned reflex learning, sign learning, trial-and-error learning, and higher forms of learning. (2) The theories of learning fall into two groups: reflex-arc theories and field theories. The reflex-arc theories subdivide further into conditioned reflex theories and trial-and-error theories. The field theories are Gestalt or near-Gestalt in character.

The conditioned reflex theories assume that all learning reduces to conditioned reflexes. In the case of the higher forms of learning, they assume hypothetical symbolic processes, which will also obey the laws of conditioning. The basis for criticism of such conditioned reflex theories, from the point of view of the present writer, lies in the fact that the learned response is practically never, save in the strict conditioned reflex set-up, the same response as that made to the unconditioned stimulus. Rather, the learned response is usually new and varies appropriately with the spatial and temporal or other interrelations between the two stimuli.

The trial-and-error theories assume that all learning reduces to the stamping in of one among an initial alternative array of *R*'s in relation to one and the same *S*, and the dropping out of the other alternative *R*'s. This type of theory as originally stated by Thorndike assumed two fundamental laws—the "Law of Exercise" and the "Law of Effect." But in his latest formulation of the theory, he has shown the "Law of Exercise" to hold only in certain restricted senses. The "Law of Effect," however, has been retained (although modified on the side of annoyers), and there has been added a new law—the "Law of Belongingness." The chief dif-

faculties with the trial-and-error theory, from the point of view of the present writer, are to be found in the facts of "latent learning." These facts indicate that learning is not a matter of direct and immediate connections between *S*'s and *R*'s. In learning, the animal learns "what leads to what." But the animal will show this learning in its performance (that is, in its *R*'s) only if its motivation at the moment so demands.

The field theories assume that behavior is mediated by organized, Gestalt-like patterns of adjustment that intervene between stimulus and response. Lashley points out the cortical character of these adjustments. Wheeler emphasizes their energy relationships and the "Law of Least Action." Köhler and Koffka emphasize the conscious Gestalt character of such adjustments and the phenomenon of "insight." Adams, following Lewin, describes them as psychobiological fields. And the present writer asserts that such "fields" contain "sign-gestalts," and that it is these sign-gestalts primarily which are made and remade in learning. All the adherents of the field theories conceive learning as involving reorganizations within such fields. They differ only in details.

For the present writer, the principal laws determining the reorganizations (or, as he would state it, the making and remaking of the sign-gestalts) would be: the "Law of Exercise," in the sense of the frequency and recency with which the "sign" and the "significate" and the "behavioral relation between the two" have been presented; the "Law of Belongingness," in the sense of the degree to which these three factors are presented under conditions that make them naturally adhere together in a Gestalt; a possible "Law of Motivation"; "Dynamic Gestalt Laws," whatever they may prove to be, which will hold in general for the establishment of fields and for the interaction among parts of fields; and finally, whatever further laws (possibly "Laws of the Possession of Symbolic Capacities") may also prove

necessary to explain the abilities required to operate with temporally absent signs and creatively inferred significates.

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CHAPTER XIII

Individual Differences

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Introduction

INDIVIDUALS are classed together as belonging to a single species when they possess common characteristics and when the "average individual" of the species differs significantly in these characteristics from the "average individuals" of other groups. The intensive study of the average behavior of a species, however, generally leads the comparative psychologist to ignore the more interesting and important differences between individuals from whom the "average individual" is abstracted. The "average individual" is, in fact, a man-made fiction, and the behavior of a species can properly be understood only by considering the variations in behavior of all (or of a random sample of) the individuals who are classed in it. Indeed, the very origin of a new species presupposes wide differences between individuals produced in overabundant quantities and struggling and competing for existence, the consequence being a selection of the more successful. The peak of mental evolution represented by man presupposes the existence of wide behavior differences among individuals of lower species.

It would thus seem natural that one of the main interests of the comparative psychologist would be individual differences in behavior. Yet adequate scientific studies of

individual differences among men began only about three decades ago, with the origin of the mental test movement, and such studies among subhuman forms have been undertaken only within the last ten years. The reasons for this long delay are the fact that the problems to be attacked were not clearly envisaged and the fact that the adequate experimental-statistical techniques were not available. The problems and the techniques are now, however, quite apparent, with the consequence that in recent years a rapid development of research in individual differences is evident. The purpose of this chapter is to acquaint the student with the problems, techniques, and evidence collected to date. We shall confine our study of evidence to that collected on subhuman forms, but the problems and techniques are truly comparative, being as pertinent to the human being as to lower species.

The psychological and quantitative principles employed in an adequate study of individual differences.—Psychologists classify the dynamic behavior adjustments of a species into rather arbitrary categories (learning, sense-acuity, drive, and so forth) to which we give the label “behavior-domains.” Each of these domains is an abstraction referring to some aspect of adjustment and can be further re-analyzed into “sub-domains.” Thus, the behavior-domain “learning” refers to the propensity of the individual to improve in adjustment to the same situation apart from the effects of maturation, and it can be subdivided further into maze learning, problem-box learning, sensory-sign learning, and so forth. To avoid confusion due to differences in terminology, one should think of behavior not in terms of the more broadly defined abstractions but in terms of the actual situation in which it is manifest. With these preliminary cautions in mind, we may examine certain principles employed in the experimental study of individual differences.

- (1) *The behavior-domain to be studied should be defined*

as a specific measure of behavior in a given situation. Thus, instead of labelling the performance on a maze "maze ability," an abstraction which implies that what is being measured is *general* capacity to learn all kinds of mazes, it is best to define the behavior specifically, for example, "total blind entrances in a given 10-unit T-maze during 30 trials under experimental conditions, *K*," *K* being fully described. For brevity, one may, of course, call the behavior "maze learning," *provided* one retains the mental reservation that one means only this particular maze behavior.

(2) *The "validity" of a measure depends upon whether the behavior measured satisfies the broad definition of the domain.* Thus, an experimenter may contend that he is measuring differences in "visual acuity," but his measure may be considered a valid measure only if by an *a priori* psychological analysis he shows that the situation elicits differences in acuity *per se*. Later we shall see, for instance, that what is measured in a discrimination-box seems, on analysis, to be visual sign *learning* rather than visual acuity. It appears, therefore, that upon the analytical acumen of the experimenter the proper estimating of the "validity" of a measure of behavior depends.

(3) *The situation that elicits the measured behavior should be adapted to the sensory-motor equipment and "natural" behavior-patterns of the species.* All of the available experimental and observational data on the species should be brought to bear on the devising of suitable "test" situations. Fowls have good vision and live in open spaces, but rats have relatively poor vision and live in closed-in spaces; each species has its idiosyncrasies, and test situations devised to study individual differences in the sundry behavior-domains should be adapted to these idiosyncrasies.

(4) *The "universe" of subjects and the experimental group of individuals drawn from it should be defined and the nature of the selection made known.* Ideally, one

would wish to study a random sample of the whole species, but to do so is ordinarily impossible. Usually, one has to use the laboratory stock available, and whether this stock is a random sample or is inbred or selected for certain characters is rarely known. Lack of knowledge on this score is a crucial deficiency, for obviously, if the stock derives from an inbred strain, all the individuals tend genetically to be the same, and hence, individual differences may not appear. A *definition* of the *stock* from which the observed sample is drawn should include a statement of its origin and the degree to which it has been inbred. Regarding the *sample* of individuals studied, a statement should be made as to the nature of selection from the stock; that is, if it is a random selection, it should be so described—or the number of litter-mates used should be given; and the age of individuals, their previous experience, and the number of individuals should be stated.

(5) *Two comparable measures of the behavior-domain should be secured for each individual in order to ascertain the extent and consistency of individual differences.* The importance of this requirement will be made apparent by a concrete illustration. Suppose our problem were to study individual differences in the domain “blind-alley entrances in a given 10-unit T-maze during 30 trials.” We have chosen our sample of rats and have run them on the maze. Rat *A* turns out to be a poorer learner than Rat *B*, making considerably more errors than *B*. Is this difference a consistent, that is, a reliable, difference? To answer this question, we need two comparable measures of this domain for both *A* and *B*. The method ordinarily used is to add up the errors made by each on odd trials, 1, 3, 5, . . . 29, and note in the totals the difference between *A* and *B*. Then for each rat, we add up the total errors made on even trials, 2, 4, 6, . . . 30, and note the difference. Thus, we obtain two comparable measures for both *A* and *B*, and if *A* is equally poor in both measures as compared with *B*, we

know that the difference is consistent and reliable. Of course, in practice, we would secure the total odd and total even scores for all rats in the group and calculate the correlation coefficient between the two series of scores. If r (the coefficient of correlation) is 1.00, we know that individual differences are perfectly consistent and reliable; if r is 0, we know there is no consistency and that reliable differences between the animals are utterly absent. The magnitude of the correlation between the comparable measures is thus a measure of the degree to which consistent individual differences *exist* under these conditions of measurement. Until we find this degree, few of the problems of individual differences can be attacked, for, it should be apparent, the degree to which individual differences are correlated on two comparable measures of the *same* domain will radically affect the correlation between this domain and other different variables.

(6) *The analysis of the results should be succinctly stated by means of adequate statistical formulæ devised for this purpose.** A concise statement of the *spread*, or variation, among individuals is the *standard deviation* (sigma) of their scores. The measure of the degree of reliability of individual differences in a behavior variable X is the *reliability coefficient* r_x , which is defined as the correlation coefficient between scores in the given domain and those in an exactly comparable domain.†

* Limitations of space will not permit of our reviewing the elementary statistical formulæ mentioned here. If the student has forgotten the meaning and uses of standard deviation and the correlation coefficient, it is suggested that he refer to any standard statistics text, such as Garrett.⁽⁶⁾ For a brief account of methods pertaining to the reliability of individual measurement, see reference 6 in the bibliography, Chap. VI, pp. 266-274.

† According to this definition, the correlation between errors on *odd* and on *even* trials, r_{oe} , is not the reliability coefficient of errors on *all* trials but only of those on a sample of half the total trials. The reliability coefficient of total trials can be estimated from r_{oe} by the Spearman-Brown formula, $r = 2 r_{oe} \div (1 + r_{oe})$. (Garrett (6:271))

The problems to be attacked in the study of individual differences.—There are four major problems to be solved in any complete attack on individual differences in any given behavior-domain. These are: (1) To what extent are individuals *consistently* different from each other, and how *constant* are these differences throughout their lives? (2) To what extent are these differences related to physiological and morphological differences? (3) To what extent are these differences caused by differences in hereditary constitution rather than by differences in experience? (4) To what extent are individual differences in the one behavior-domain related to (that is, correlated with) individual differences in other behavior-domains?

We turn now to a consideration of the experimental evidence bearing on these problems.

The Evidence Bearing on the Problems of Individual Differences

Evidence relating to the stability of individual differences.—In evaluating the experimental evidence on consistency, certain factors must be kept in mind. First, the spread and the reliability coefficient will be greater the more nearly the experimental group approximates a random sample of the whole species. Second, a higher reliability will result from a more thorough measure of each individual: for example, in maze measures, from more blinds, a more complex pattern, and more trials; in sensory discrimination measures, from more trials or discrimination points, and so forth.*

In the following treatment, we shall review the evidence as it bears on the two subproblems (1) extent and consistency of individual differences in various behavior-domains

* This principle is embodied in the Spearman-Brown formula, which is really a law of individual measurement. There are other important factors affecting consistency; for a more extended account, see references 28, 37, and 41 in the bibliography.

and (2) constancy of the differences over varying intervals of time. Most of the evidence is drawn from but one species, the rat; but this is due to the unfortunate fact that no adequate work has as yet been done on other species (except man).

(1) *Learning.* (a) *Maze learning.* For an experiment, the writer chose a random sample of 141 pied and albino rats from two large heterogeneous laboratory colonies, neither of which had histories of inbreeding. These animals were run on two long, difficult T-mazes, the first (Maze X) possessing 17 blinds, and the second (Maze Y) possessing 20 blinds. The procedure consisted in an initial run of 11 trials on a "practice path" involving no choice points, 19 trials on Maze X, a week's rest, 5 practice runs, and then 19 trials on Maze Y. The reward was food, and one trial a day was given.⁽⁴¹⁾

Marked and consistent individual differences were discovered. The reliability coefficients for errors on trials 2 to 19 were .99 for Maze X and .97 for Maze Y. For a sample of 45 animals who relearned Maze X (13 trials) some months later, the reliability coefficients of successive periods of only 6 trials each were .94, .98, and .98 for original learning, and .95 and .97 for relearning.⁽⁴⁴⁾ At the end of relearning, the last two periods of only 4 trials each gave coefficients of .95 and .97.⁽⁴⁵⁾ Here is evidence of as consistent individual differences in these domains as are found in human "intelligence" domains.

The *constancy* of individual differences throughout the whole experimental period is indicated by the correlation between *different* trial periods. On a random sample of 107 rats, trials 2 to 19 were divided into stages of 3 trials each, and intercorrelations between total errors on these 6 stages calculated.⁽³⁹⁾ All these coefficients cannot be given here, but in Table XV are given the average of correlations between each stage and its preceding and following stages of learning and similar coefficients for the first 4 single trials.

Note that as time proceeds during the experimental period, the coefficients rise and reach very high magnitudes. This means that with practice individual differences become stable. This emergence and stabilizing of individual dif-

TABLE XV

AVERAGE r 'S BETWEEN A GIVEN PERIOD (TRIALS AND STAGES) AND ADJACENT PERIODS OF LEARNING FOR THE CONSECUTIVE PERIODS IN THE LEARNING OF TWO MAZES

Trials	<i>Single Trials</i>				<i>Stages Consisting of 3 Trials</i>					
	1 ¹	2	3	4	(2, 3, 4) ¹	(5, 6, 7)	(8, 9, 10)	(11, 12, 13)	(14, 15, 16)	(17, 18, 19) ²
Maze X	.14	.36	.64	.75	.72	.81	.91	.92	.92	.93
Maze Y	.05	.31	.59	.65	.71	.78	.81	.75	.78	.83

¹ In the case of Trial 1 and Stage (2, 3, 4), there was no preceding period present, so that the r given is the correlation with the following period.

² For Stage (17, 18, 19), the r is the correlation with the preceding stage only.

ferences is shown very clearly in the coefficients of even the first 4 single trials.

But how constant are these differences throughout the lives of the animals? This question is analogous to the problem of the constancy of the I. Q. in human beings. Three different groups of animals were used to investigate this matter.⁽⁴⁴⁾ The procedure was to run them 19 trials on Maze X, and then after a long interval of time to run them again 13 trials. During this interval, all the animals experienced breeding conditions; furthermore, Group I ran another maze, and Group III changed quarters from one building to another, relearning under the new conditions. Statistical evidence indicated that the three groups had dispersions in original learning similar to a random sample.

Full data are presented in Table XVI, *L* (learning) being total errors on the first 19 trials, and *R* (relearning) being the total on the second 13. The correlations between learning and relearning are .80 or higher, indicating a very high degree of constancy over an interval of from 6 to 8 months, which is more than a third of the rat's life span. Even

TABLE XVI

THE CORRELATIONS BETWEEN LEARNING AND RELEARNING OF A MAZE
FOR THREE GROUPS OF RATS EXPERIENCING
DIFFERENT INTERPOLATED CONDITIONS

Group	N	Interval between Learning, <i>L</i> , and Relearning, <i>R</i> .		Reliability Coefficients		Correlation between <i>L</i> and <i>R</i> ¹		
		No. of days	Conditions	<i>L</i>	<i>R</i>	Raw	True	
		<i>M</i>	<i>S. D.</i>					
I	46	232	19	Breeding, Maze Y	.99	.98	.79	.81
II	25	196	28	“ “	.99	.98	.79	.81
III	36	196	51	“ new quarters	.98	.96	.85	.88

¹ The raw correlation is simply r_{LR} ; the true correlation is r_{LR} corrected for attenuation. See reference 6 in the bibliography, p. 211 ff.

between scores on the *first* 6 trials of *L* and the *last* 6 trials of *R*, the raw correlation was found to be .81 (true .85), and this was the correlation between two periods each involving less than 15 minutes of running but separated by a considerable portion of the rat's life.

The above facts are corroborated by experiments on Stone's 12-blind T-maze. Stone and Nyswander ⁽³³⁾ ran 205 rats from Slonaker's *inbred* stock* 30 trials through

* In this experiment and in other experiments reported below, the group of animals is frequently reported as being drawn from an "inbred" stock. Whether this means that all the animals were from the *same* inbred line or consisted of different subsamples from each of *different* inbred lines is rarely reported. The existence of such marked differences between individuals suggests that the latter condition obtained.

the maze. The reliability coefficients were .95 both for total errors and for total time. Even for successive 10-trial stages, the reliability coefficients were .78, .94, and .94 for errors, and .91, .97, and .87 for time. Using the same type of maze and the Wistar inbred stock, Leeper⁽¹³⁾ ran 34 rats (Group C) 30 trials, and for errors found a coefficient of .94. These experimenters used food as the reward, but Ruch,⁽²⁰⁾ who used escape-from-water as a drive, found (with 19 inbred animals) a coefficient of .95. Had these animals been more definitely a random sample of rats, the reliability coefficients would doubtless have been even higher. Using more representative samples, Tolman and Honzik⁽³⁵⁾ ran several groups of rats on a modified Stone maze and found wide differences even when *no reward* was given. For two such groups, one hungry and the other slightly hungry, the reliability coefficients for 17 trials were, respectively, .97 and .86 for errors and .97 and .88 for time; and for two analogous groups rewarded by food at the maze-end the coefficients were .96 and .85 for errors and .99 and .95 for time. Even for a group that received reward during certain trials and then had it withdrawn during others,⁽³⁶⁾ the coefficients for the nonreward period were of the order of .92 and, for the reward period, .96. Thus, under quite extensive variations in motivation, consistent differences in performance appear.*

* We cannot go into the details of other experiments on consistency in maze learning, but below is a brief survey of the reliability coefficients found by other workers: On the 10-blind Carr maze, Stone found .75 on 20 trials.⁽³²⁾ On a 2-blind maze, Alm found .92, .93, and .93 for three groups.⁽¹⁾ Miles used two 15-blind T-mazes, one on the floor and the other elevated, and found coefficients of .86 and .84.⁽¹⁸⁾ Corey's group on an 8-blind elevated maze gave coefficients of .89, .96, and .92 for errors, total time, and active time, respectively.⁽⁴⁾ Liggett's group, which ran a 4-unit linear maze, gave .92 and .90 for time and errors, respectively.⁽¹⁴⁾ Using 6 Warner Y-units, Jackson found coefficients of .76 and .95 for a simple- and a double-alternation pattern, respectively.⁽¹¹⁾ Husband⁽¹⁰⁾ used 10 Warden U-units and found a reliability coefficient of .88. This array of high coefficients proves conclusively the universality of consistent individual differences in maze ability among rats.

Some of the coefficients given above and throughout the text are not

Stone and Nyswander⁽³³⁾ found also a high degree of constancy throughout the experimental period, the raw r between total errors on Trials 1 to 10 and total errors on Trials 11 to 20 being .75, and the true r , .86. McNemar and Stone⁽¹⁷⁾ found as high a degree of constancy of individual differences as this over intervals of from one and one-half to four months. Their procedure was to run the animals 30 trials on the maze, and then after an interval of time during which the animals worked on other apparatuses, to run them again 15 trials. A number of groups were run, but for our purposes, we shall consider only those that showed the greatest spread in original learning. Two groups (C and F) that experienced a problem box and a visual discrimination box during the 45-day interval between the two maze series both gave r 's of .80 between learning and relearning error scores; two other groups (H and K) that experienced only the problem box during a 125-day interval gave, respectively, coefficients of .89 and .75. Here, again, is evidence of the high constancy of individual differences over a fairly long interval of time.

(b) *Problem-box solution.* The measure of efficiency in problem-box solution is time. Heron found, with his simple inclined-plane box, a reliability coefficient of about .8 for total time for trials beyond the first 8.⁽⁸⁾ Using 98 inbred animals, who worked on a single-treadle box, Stone found, excluding the first 5 trials, a coefficient of .76,⁽³⁰⁾ and, when a box in which the animal had to consider three treadles before getting out to food was used, a coefficient as high as .83.⁽³⁾

(c) *Sensory cue learning.* Before we can present problems that legitimately measure the behavior of animals, it is desirable to know the animals' sensory-motor capacities. Of paramount importance is knowing the classes of stimuli

those reported by the authors, who in certain instances failed to apply the Spearman-Brown correction and in other instances applied it wrongly. Throughout this chapter, the writer has made the proper corrections.

or stimulus-patterns to which the animals are sensitive—and especially we want to measure individual differences in their sense acuities. But the typical discrimination-box does not measure such individual differences. In a visual discrimination box, for instance, the animal is presented with a light path and a dark one, and he must learn to go through one and not the other. Here, the stimulus difference is within the threshold of all animals, and, therefore, what is measured by total errors is capacity *to learn* to follow one stimulus and avoid the other. This is sensory sign *learning*. To measure acuity differences, it is necessary to wait until all the animals have learned the first difference in intensities, and then on later trials gradually to reduce the difference between the two stimulus intensities until the learning breaks down. Individual differences in visual acuity will then be defined as the stimulus difference at which the animal's learning breaks down.

The notable work on visual sign learning is that of Stone.⁽²⁹⁾ Seventy-one rats ran a 5-chamber light-dark box for 40 trials. The reliability coefficient of errors from Trials 11 to 40 was .94, and the coefficients of successive stages of 10 trials each were .51, .87, .82, and .93. Similarly, Williams⁽⁵²⁾ found, on a one-chamber box and with two groups of rats, a coefficient of .96 for errors on 24 trials. In kinæsthetic cue learning (requiring the discriminating of different inclined paths), Ruch's 24 animals gave a coefficient for errors on 40 trials of .79.⁽²¹⁾ As to the constancy of such differences, Stone⁽²⁹⁾ discovered that between the last three stages of 10 trials each, the raw r 's were .71, .75, and .85, the true r 's being .79, .89, and .98. From these and the above data, it appears that individual differences are both consistent and constant in these domains of learning.

(2) *Capacity to discriminate stimuli or stimulus-patterns.* The conditions for measuring acuity were indicated above. To the writer's knowledge, no analyses relative to the prob-

lems of *individual differences* have been carried on under these conditions. Yoshioka's work on the discrimination of distance ⁽⁵⁵⁾ is, nevertheless, relevant here. He ran rats in a box in which food was reached through a long or a short path, where the ratio of long to short was the value R . The score was the number of choices of the short path, and the reliability coefficients of the total scores on 54 trials for five different groups (of 40 rats each) with different R 's are shown in Table XVII. High consistency of individual per-

TABLE XVII
RELIABILITY COEFFICIENTS OF RATS' CHOICES IN A DISTANCE
DISCRIMINATION APPARATUS

Group	I	II	III	IV	V
R	1.44	1.33	1.23	1.14	1.07
Reliability coefficient ¹	.82	.93	.82	.92	.83

¹ These r 's are mean r 's of animals running to the same R on Yoshioka's mazes I and II.

formance is apparent in these domains. In Group V, where the short path was almost equal to the long path, Yoshioka found that the mean of short choices was about equal to that of long choices, indicating no discrimination. Why is there such high consistency here, where one would think that the rats were running by chance? The reason is that they tended to form *position-habits*, and since the short path was always on the same side for each rat, if he had a position-habit for this side, he consistently secured a high score; if to the long side, he consistently earned a low score. Thus, the coefficient for Group V indicates the high consistency with which the animals *form a position-habit* in a nondiscriminable situation. But the rats of Group I showed a marked learning of the short path, so that here we have evidence of high consistency of learning "shortness" as a means-end relation involving least effort in reaching

food. Just how to get a measure of individual differences in distance discrimination out of such data is not apparent. In an analogous experiment where the animals were faced with the problem of discriminating kinæsthetic *patterns* of equal length, that is, a 1-triangle path and another path of equal length but consisting of a number of triangles, Yoshioka found high consistency as indicated by reliability coefficients for different groups of .95, .83, .85, and .94, though here again, the differences may have been largely due to position-habits rather than discrimination capacity.⁽⁵³⁾

(3) *Drive*. Little work has been done on individual differences in the strength of the various types of biological drives.* One interesting approach is that of Washburn,⁽⁵¹⁾ who measured the degree to which mice were hunger-driven by correlating for each mouse the amount of food eaten at the end of a maze (Watson's circular maze) with his velocity of running. The r 's for different mice ranged from .76 to zero. Those whose r 's were high were called "hunger-driven," those whose r 's were low, "activity-driven." This is an ingenious motivation scale, and all the problems of individual differences in this domain should be attacked by its use, though on better mazes and with more animals. Differential studies should also be advanced by the use of the obstruction-box, which has been shown to have considerable value in the measurement of different types of drives.⁽⁵⁰⁾

The most complete work on individual differences in gross energy has been done by the measurement of it in rats by the number of revolutions they make in circular revolving cages. Using, apparently, a fairly random sample of animals, Shirley found great differences between individuals.⁽²⁵⁾ Over a period of days, some rats showed a median distance travelled per day of about 8 *miles*; others of as

* Cf. Chapter IV for heretofore unpublished data collected by Stone.

little as 180 feet. For periods of 5, 10, and 20 days, the reliability coefficients of revolutions were .97, .98, and .99, respectively. The constancy of these individual differences was also quite marked. Over a period of 15 days, the correlations between *different* 5-day periods were .89, .88, and .95. Even when a considerably greater interval elapsed between measures of activity, the correlations were very high.⁽²⁶⁾ Thus, with rats who were given a 10-day run at the sixth, seventh, eighth, and ninth months of life, the *r*'s between the sixth month's record and the records of the seventh, eighth, and ninth, respectively, were .88, .81, and .72; between the records of the eighth and ninth months, .86. It was also apparent that as the rats grew older, the differences between them became more stabilized. Another measure of activity that showed the same fact of consistency was that obtained by Hall,⁽⁷⁾ who placed the rat in a circular laboratory field where the food was in the middle but enclosed by a barrier. For 26 males and 26 females running 14 two-minute periods, the reliability coefficients of total distance travelled were .89 and .96, respectively; with the barrier removed, the coefficients were .93 and .93. Another interesting discovery was that rats differed consistently in "appetite": the reliability coefficients for "amount of food eaten" were .99 and .93, respectively.

(4) *Emotional expression.* How to provide standard stimulus situations in which directly to measure differences in anger, fear, and other emotional reactions has been a problem. One adequate quantitative analysis is that of Hall, mentioned above, who measured differences in certain correlated by-products of the fear reaction. When rats show marked fear, this state is usually accompanied by urination and defæcation. Hall kept counts of the defæcations and the urinations per rat during the first trials and found very marked, consistent differences, as indicated by the following reliability coefficients for males and females respectively: defæcations, .83 and .96; urinations, .86 and .96.

Whether differences in elimination frequencies represent accurately differences in degree of emotional upset is not as yet definitely known.

Evidence bearing on the relation between behavior differences and physiological differences.—Little work has been done with animals on the relation between normal behavior differences and differences in somatic structures or functions, although this is obviously a problem of great interest and importance. The numerous experiments on the effect of cerebral insult on behavior (by Lashley, and others) do not bear directly on this problem. What we want to know here is the correlation of behavior differences among *intact* animals with their differences in physiological and morphological make-up. Work that has been done has been that with reference to obvious morphological differences.

(1) *Age and behavior.* In a previous chapter, the relation between physiological maturity and behavior was discussed, and we will not review it here except briefly to recall that in the researches of Stone on this problem, he found that for rats, in many learning domains, there was no relation between ability and age (from puberty to early senescence).^(30, 31)

(2) *Sex and behavior.* In human beings, it has appeared to be a universal fact that, other things being equal, there is a negligible difference between males and females in cognitive capacities. And the findings in subhuman animals have been similar. In his T-maze studies mentioned earlier, the writer found a slight indication of male superiority in learning, but this difference was negligible with respect to the vast differences between individuals due to other factors.⁽⁴²⁾ Studies from the Stanford laboratory^(16, 38) give similar results. Rats were given trials on a T-maze, a Carr maze, a problem box, Warden U-mazes, light-dark discrimination boxes, and two elevated mazes. Either no sex difference was found in these different experiments, or where a slight

male superiority was indicated, it was negligible relative to the great overlap of the two sex groups. It seems very probable that if a behavior difference between the sexes exists, it will be in emotional domains. In human beings, measurements of neuroticism by the Thurstone personality inventory and those of annoyance by Cason indicate that in these domains a very evident difference between the sexes appears, and it is significant that also in the experiments by Hall on emotionality in rats, very evident sex differences appear. Greater activity has been noted in the female,^(9, 19) the predominance being greatest at the peak of the sexual cycle.⁽⁴⁹⁾

(3) *Other morphological characters.* From the very slight amount of work done on the relation between other morphological characters and capacity, no evidence has appeared to indicate that such characters are predictive "signs" of ability. Even when one might have expected some relation, none has appeared. For instance, in the writer's experiments, the animals all received the same amount of food, and since they differed considerably in weight, one might have expected that the animals were being differently rewarded and that this fact would affect their maze scores. But the correlations between weight and error scores proved to be zero. Again, one might have expected that pied rats with pigmented eyes would have been, by virtue of superior vision, superior to pink-eyed albinos in maze-learning. Yet here also, only a negligible difference in ability appeared.⁽⁴²⁾ In nondiscriminable situations where rats show position-habits, Yoshioka found an r of $.43 \pm .15$ (S. D.) between number of right choices and degree of right curvature of the nose, indicating a slight tendency for a rat to "follow his nose."⁽⁵⁴⁾ Shirley studied the relation between activity and body weight,⁽²⁷⁾ and found zero correlation. The brains of the animals were weighed and the correlations between activity or maze ability with

weight of cerebrum or cerebellum or per cent of brain weight were all unreliably different from zero.

Apparently, the real causes of behavior differences are exceedingly numerous, complex, and fundamentally related to differences in the integrations in the nervous system and its projecting sensory-motor tissues, so that any differences attendant upon simple differences in external gross morphology are readily swamped by these more fundamental sources of variation.

Evidence indicating the degree of causation of individual differences by hereditary and by environmental factors.—Since the beginning of the twentieth century, geneticists have accumulated considerable data on the genetic causes of individual differences in morphological characters in plants and animals. Few controlled experiments have been performed on behavior, doubtless because, until recently, no one knew how to measure mental differences accurately. Thanks to the work of the geneticists, the methods of studying hereditary causation are now evident. To study hereditary causation of mental differences, it is necessary (1) to choose as the original experimental population, P , a random sample of animals from the species, (2) to measure accurately the behavior differences of these on a valid scale and under rigorous conditions of environmental control, and then (3), by sundry systems of mating, to determine the nature of the hereditary factors at work. To study environmental causation of differences, it is necessary (1) to choose a group of individuals all exactly identical in heredity (a "pure line") and (2) from these to select random subgroups, $S_1, S_2, \dots$, which are then respectively exposed to different environments, $A_1, A_2, \dots$, the latter being systematic variations of an environmental condition, A .

(1) *The objective facts from controlled experiments.*—(a) *Selective breeding studies.* To what extent are individual differences in maze learning due to hereditary determiners? Using the method described just above, the writer

endeavored to establish, through selective breeding by assortative mating, two races of rats, a "bright" and a "dull." ^(46, 47) A random, unselected sample of 142 rats was chosen and then run for 19 trials on Maze X, described earlier in this chapter. The measure of learning capacity was the total errors on all trials. Figure 66 shows the results of selective breeding for brightness and dullness. The error scale across the top refers to all generations below it, the extreme left end being the "bright" end of the scale (few errors) and the extreme right end being the "dull" end. The frequency distribution of the original *P* group is just below the scale. Note the extreme dispersion of individuals and the unimodal distribution. Extremely bright (B_p) individuals were bred together, and their progeny are shown below—indicated as the F_1 (first filial) generation. The F_1 progeny of extremely dull and median ($D_p + M_p$) are also shown. Not much difference appeared in this generation. The assortative mating of extreme bright and of extreme dull was continued, and the results show a gradual appearance of a bright race and a dull one. In the F_8 , there is practically no overlap between them. These are the results at present date, and it appears that we are finally approximating two pure lines, one which "breeds true" for brightness and one which "breeds true" for dullness. It is apparent, therefore, that differences in this maze ability are markedly determined by differences in hereditary constitution.

It is to be recalled that Shirley found differences in the activity of rats to be wide and consistent. That such differences are markedly due to hereditary differences is now apparent from the experiments of Rundquist, who after 12 generations of selective breeding established a race of active and one of inactive rats.⁽²²⁾ Other experiments on behavior inheritance have been performed, but in these no evidence

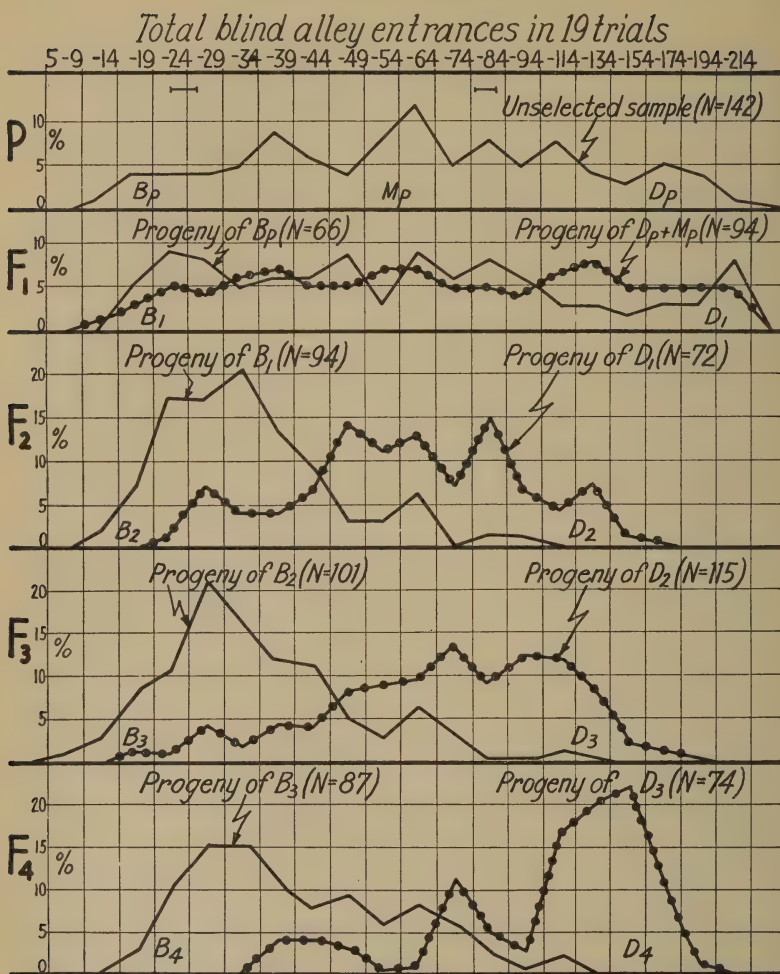


Fig. 66.—Effects of Selective Breeding on Maze Learning.

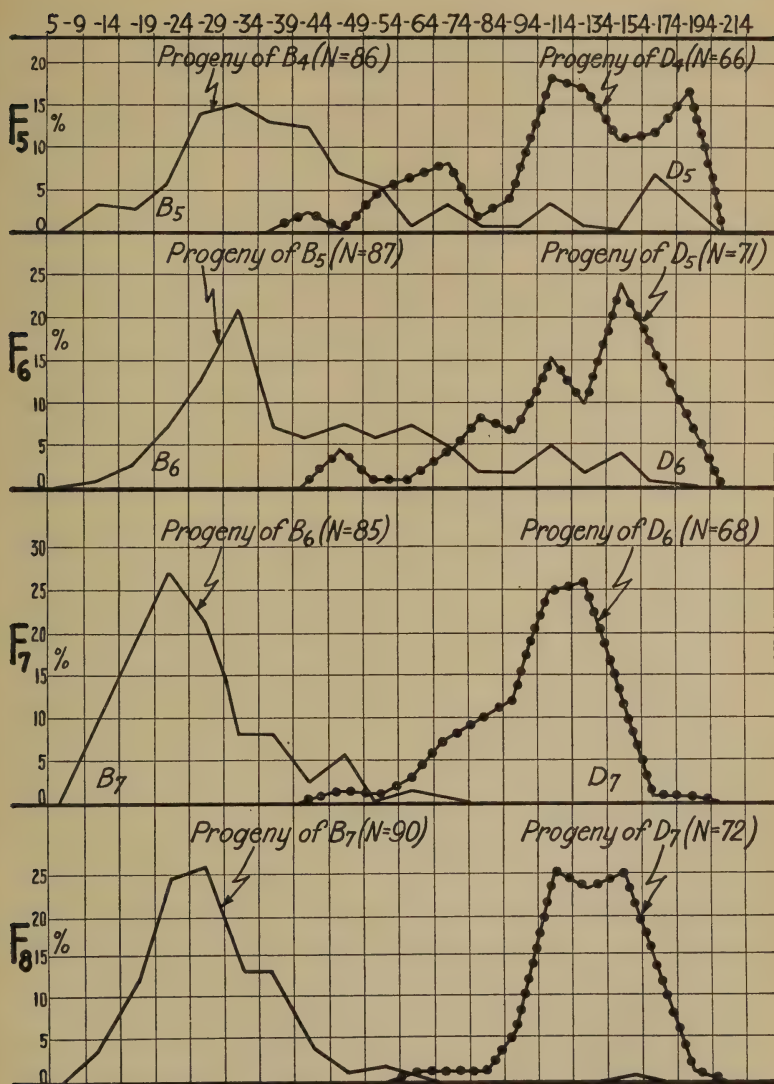


Fig. 66.—Effects of Selective Breeding on Maze Learning.
(Continued)

as to the consistency of individual differences has first been secured.*

(b) *Family resemblance studies.* A common method of studying inheritance is that of determining the correlation between groups of individuals of different degrees of relationship, such as identical twins, fraternal twins, siblings, and parents and progeny. Such methods are relatively inconclusive, since the coefficients are delicately affected by the degree of assortative mating and selective breeding in the populations. For example, it is apparent from the facts of Figure 66 that the correlation between parents and offspring depends on the *degree* of selective breeding: for example, between P and F_1 , the r would be low; between F_7 and F_8 , it would be very high.

(c) *Effects of varying environments on individual differences.* Another method of approach is to raise a group of individuals under a constant environment, then measure differences between them in a given behavior; next, expose them to variations in environment, and then re-measure them in the given behavior. If the correlation between the two measurements is very high, it indicates that the environmental variations are relatively unimportant in affecting behavior differences, and that the differences are therefore primarily determined by heredity. Experiments of this type by Stone and the writer were reported earlier under the heading, "Evidence relating to the stability of individual differences," where it was shown that the correlation between the learning and the relearning of a maze by rats was very high even though great environmental changes were introduced † during the interval between the two measurements.

(d) *Studies relating to the Lamarckian hypothesis.* The

* See references 2, 23, 24, 34, and 48 in the bibliography.

† With this method there are numerous difficulties, which space limitations prevent us from discussing here. For an account of these, see reference 44 in the bibliography.

Lamarckian view that differences in behavior may be due to differences in the experience of the parents which are transmitted to the offspring in the form of "biological memory" has been experimentally tested—generally, with negative results. To test this theory, the following technique is mandatory: (1) the task to be learned must be important to the animal and must be tackled by him under strong motivation; (2) all animals of the initial population should be exactly the same genetically (a homozygous, inbred stock); (3) successive generations must be put through the task under exactly the same experimental controls. This technique being followed, if "biological memory" is a fact, later generations should perform better than earlier ones. The second condition, genetic identity, is crucial, for without it, the improvement in later generations may result from selective breeding. McDougall's experiment is a *behavior* study testing this theory.⁽¹⁵⁾ Using animals from the inbred Wistar stock, he put them through a water discrimination-box in which in the lighted alley the rat had to climb over an electric grill giving sufficient shock to tetanize the muscles, whereas through the dark alley it could escape without shock. McDougall found in later generations marked improvement in learning to avoid the lighted alley where the shock was given. One explanation of these results on grounds other than the Lamarckian hypothesis is as follows: the rats may not have been identical genetically, but rather, may have varied widely in innate learning capacity (in one group, the learning scores varied from 90 to 229); the electric shock may have constituted a selective agent by its severity* and frequent repetition, either eliminating the stupid animals or occasioning full or partial sterility among them. Thus, the results may have been due to the selection of bright learners.

* See the abstract of the work of Dunlap on the physiological effects of electric shock.⁽⁵⁾

It is of interest to note that in the writer's experiments (see Figure 66), no Lamarckian effects are to be discerned in the dull race, for the dull F_2 are as dull as the dull P animals.* A final difficulty with this hypothesis is that no mechanism has as yet been conceived of whereby the *specific ideas* of parents can be transmitted through the germ plasm to the offspring, whereas the mechanism of Mendelian factors or genes is quite adequate to explain selection, as the next section will indicate.

(2) *Factor explanations of the objective facts.*—(a) *Genetic (hereditary) factors: the Mendelian factor theory.*† It is to be recalled that the theory of mental evolution demands wide inherited differences in behavior between individuals, and that the above experimentally determined objective facts indicate that such differences do exist. And it is to be noted that individuals exist in all degrees of capacity, forming, in fact, a continuous unimodal distribution. What biological mechanisms exist to explain these objective facts? The most adequate theory, supported by many genetic investigations of plant and animal structures, is the theory of *independently assorting multiple Mendelian factors (or genes)*. We shall describe this theory by showing how it may account for individual differences in maze-learning ability. It is assumed that there is a large number, k , of genes determining this ability. First, consider one of these genes, A , which exists in two degrees of expression, A and a . An individual of homozygous constitution, AA , is brighter than one of aa constitution, and a heterozygous individual, Aa , lies between the two. No

* A thoroughgoing Lamarckian would, however, criticize the writer's task as not being as important to the rat and causative of such striving as McDougall's, where the rats had to avoid near-electrocution.

† Space limitations preclude the presenting here of an elementary treatment of Mendelian theory, and the suggestion is offered the student either to read, say, such a brief but adequate account as that by T. H. Morgan in *The Foundations of Experimental Psychology*, pages 7–22 (edited by Carl Murchison, Clark University Press, 1929) or to skip this section.

dominance is assumed. But there are k such genes, A, B, C, D, . . . , each possessing the same properties as those described for A. Thus, an individual of constitution $AABBCCDD$. . . would be the brightest possible in maze ability, $aabbccdd$. . . the dullest, and $AaBbCcDd$. . . would be average. All degrees of ability would be possible: $aABBCCDD$. . . next to brightest, $aaBBCCDD$. . . next, $aabBCCDD$. . . next, and so on. Thus, the continuity of individual differences is adequately explained. Under random mating, the types of individual that could exist and the frequency of each can be found from the product of $(A + a)^2 (B + b)^2 (C + c)^2 (D + d)^2$ In the resulting series, the terms show the various genotypes, and their coefficients the frequency of their occurrence. The result is a *normal distribution curve*, if k is large enough. Hence, the wide, continuous, and unimodal dispersion of individuals in the P generation (Figure 66) whose parents were randomly mated is adequately accounted for.

According to this theory, the effects of selective breeding result simply from the gradual sorting into one race of all the large-lettered genes for brightness, and into the other, all the small-lettered genes for dullness. In a final bright pure line, *all* individuals would be $AABBCCDD$. . . , and their progeny would be exactly like them; analogously, in the dull pure line, all would be $aabbccdd$. . . and would breed true for dullness.* Some modification of this theory is necessary to account for the regression of progeny of bright and of dull. The linkage of different genes in the same chromosomes would also affect the results.

Later, we shall see that the rank order of individuals in

* Final tests of this theory will consist in the crossing of these two pure lines. If the theory is adequate, then all of the new F_1 individuals will show the *same median* capacity, since all will be of constitution $AaBbCcDd$ Selfing these F_1 's should give an F_2 , in which all the genetic types will appear; that is, the distribution should be similar to that of the P group at the top of Figure 66.

different learning domains is not the same: that the inter-correlations vary from nearly unity to zero. These facts in no way jeopardize the view that individual differences are inherited, for they may mean only that individual differences in different behavior-domains are determined by different gene-complexes. If two behavior-domains are determined by the same gene-complex, they will correlate unity (the environment being constant); if they are determined by different complexes, they will, under random mating, correlate zero. In brief, the degree of correlation will thus be determined, under random mating, by the proportion of common genes entering into the two behavior-domains.

Apart from this cause of intercorrelation, two behaviors may show positive correlation without there being common genetic factors. If, for example, behavior *X* is determined by genes A, B, C, and D and behavior *Y* by genes H, I, J, and K, no correlation between *X* and *Y* would appear from common genes, since there are none. But if some selective agency is at work to produce assortative mating in such a fashion that the superior individuals (represented by large letters) in *X* and in *Y* tended to breed together, and if, likewise, the inferior ones (represented by small letters) mated, the individuals in later generations would show a positive correlation between *X* and *Y*, since the two extreme types of individuals would be of constitution *AABBCCDD-HHHJJJKK* and *aabbccddhhiijjkk*, and the types of individuals throughout the intermediate range would have the same genes in corresponding degrees of expression. Thus, positive correlation between behavior-domains may mean either common gene-complexes, or independent gene-complexes correlated by virtue of assortative mating.

(b) *Environmental and maturational factors.* It cannot be denied that differential training may exert considerable influence in determining individual mental differences. Extreme environmentalists assert quite unreservedly that

behavior differences derive primarily from differences in conditioning, especially during early development. There may not, however, be an issue here, for even when learning proceeds by conditioning (or by any other means), differences in *capacity* to form conditioned responses may be wide and, furthermore, inherited. The laws of learning attempt to describe the process through which the individual goes from inefficiency to efficiency, whereas the laws of inheritance attempt to describe the nature of the forces which account for inherited differences in capacity to go through the learning process. The best means of studying the process of individual development is to get rid of variation due to heredity by working with individuals of the same heredity.

There are, indeed, two very different types of developmental process: learning and maturation. Innumerable experiments have been performed on the effects of learning in one situation upon that in another (transfer), of varying the situation, the motivation of learning, and so forth; but since these have been discussed in other chapters, we need not consider them here. Likewise, the nature of maturation and the factors that affect it have been treated elsewhere.

Evidence bearing on the relation between individual differences in one behavior-domain and individual differences in other domains.—To what extent is the behavior of the individual in one situation generally *characteristic* of him in all situations? If we discover that an individual manifests superior learning ability when confronted by one task, can we predict that he will be superior in all tasks? Is superior learning associated with superior sense acuity, with strong motivation, and so on? If we should find no such correspondence, may there not, nevertheless, be some *congruence* between an individual's several behaviors, or is behavior, on the contrary, highly specific, seeming to indicate that adjustment in one situation is exclusively character-

istic of the individual in that situation and in no other? Our method is to calculate the intercorrelations between performance in divers behavior-domains, and then to study the magnitude and significance of such correlations.

Intercorrelational evidence may also shed light on *the psychological nature* of the causes of the individual differences that appear in one behavior-domain. Such evidence is, of course, secondary, our main information coming from an *a priori* analysis of the situation and of the behavior *in situ*. Thus, on *a priori* analytical ground, we must present a psychological rationale that differences in maze errors are differences in *learning*, that differences in breakdown when the light intensities of alternate paths in the discrimination-box are gradually brought to equality are differences in *visual acuity*. But the correlation between these behavior-domains and other domains may occasionally shed some light on the matter. Whereas such evidence does not invalidate an *a priori* psychological analysis, it may divulge some of the conditioning psychological features of the behavior. Thus, if maze-learning scores correlate highly with degree of hunger-drive, with gross activity, with visual acuity, and so forth, these facts would inform us of some of the causes (or associated conditions) of learning.

(1) *Evidences from temporal subdivision of the same behavior-domain.* We noted earlier that high intercorrelations were found between the performance of rats on different trials in maze learning, even when such trials were separated by a considerable interval of time, and we noted that this was also true of gross activity. It was further apparent that as the animals became more inured to the situation, the intercorrelations were higher. From these scant data, we may tentatively conclude that ability, especially after inurement, is temporally a stable characteristic of the individual in a single, defined behavior-domain.

(2) *Evidence from component subdivisions of the same behavior-domain.* This is the problem of "internal consist-

ency" or of so-called "validity of a behavior item," one of the common problems to be considered in mental-test construction. Some data of this sort have been collected on maze-learning. Stone and Nyswander⁽³³⁾ found with the T-maze that for 30 trials, the r between total errors on the first 6 *blinds* and those on the last 6 was .82. Since the reliability coefficients for each group of 6 were probably in no case greater than .85, the true r must have been nearly unity. Corey found similar results with an elevated maze.⁽⁴⁾ Here is evidence of general characteristic differences within spatial divisions of the *same* general domain.

(3) *Evidence from differently defined aspects of the same domain.* Since behavior in the same situation has many aspects, it can be scored in different ways, each defined score having, of course, a different psychological significance. Thus, maze learning can be scored in terms of errors, time, number of trials necessary to achieve a criterion of perfect learning, distance travelled, and so forth. To what extent is one aspect related to the others? Between errors and time in maze learning, the r 's have been found to be .6 (Tolman and Nyswander), .9 (Corey), and .93 (Shirley). This relation is of interest as bearing on the question: To what extent is the speedy individual also the most accurate? In maze measures, the r between total time and errors is spuriously high because time is increased by the making of errors. What is needed is velocity-when-no-errors-are-made correlated with number of errors, but no evidence of this sort seems to have been reported. Between errors and trials necessary to achieve a criterion of perfect learning, the r 's are of the order .89 (Corey), .78 (Husband), and .90 (Shirley); between time and trials, .57 (Shirley) and .87 (Corey); between time and total distance travelled, about .80 (Alm). Thus, it appears that between different measures of behavior in the *same* domain, individuals tend to take the same rank order.

(4) *Evidence from studies on the interrelation between*

behaviors when the situation is experimentally altered in a controlled manner. From studies of this sort, considerable information on the generality and the psychological nature of the causes of individual differences is obtained. In a given situation, the development of individuals is permitted until each individual has reached stability of performance; then certain stimulus features are altered and the relation between individual differences under the new and the old conditions studied. If no change in rank is observed, then differences in behavior are not contingent upon response to the stimulus-features that have been varied. The writer has performed a number of experiments of this type, using his Maze X. On this maze, which is well-lighted, the rats run their normal trials without any disturbance of the maze units whatever. At the fourteenth trial, all the animals have about reached their limits of learning, and in these plateau levels, there are marked individual differences. The true inter- r 's between the trials from 14 to 19 are approximately unity corrected for attenuation, indicating that whatever the systematic causes of individual differences on these successive trials, they are the same for all these trials. Are behavior differences here due to differences in capacity to discriminate the sundry sensory cues in the pathways and/or to form simple connections between sensory signs and response, or are the differences due to differences in capacity to form "higher" abstracted or generalized direction-distance relational sets that direct the movements? With two groups of rats who had reached a plateau in their learning, the lights were turned off for several trials and the rats run in pitch-darkness. The true r 's between the lighted and dark trials were .98 and .93 for the two groups.⁽⁴⁵⁾ Therefore, visual cues and capacity to sense them apparently do not control individual performances in the later stages of learning. Other (and as yet unpublished) experiments tested other sense modes.⁽⁴⁰⁾ Some theorists argue that maze learning is

kinæsthetically controlled in the sense that the rats form serial, chained kinæsthetic conditioned responses, previous movements providing stimuli for the later ones. If this is so, then by breaking this serial chain experimentally, the performance after the break should be completely disrupted. For one group of 76 rats, T-units 3, 4, 5, and 6 were taken out of the maze, and the animals were "short-cut" from units 2 to 7. The true r between efficiency with the serial chain intact (Trial 19) and efficiency with the serial chain broken (Trial 20) on units 7 to 17 was, for errors, .94; for time, 1.00. Certainly capacity to form serial, chained kinæsthetic responses does not determine individual differences after the rats reach a plateau in learning. In a final crucial experiment on 76 animals, on Trials 20, 21, and 22 great violence was experimentally done to the stimulus situation: the lights were turned off, a blanket was thrown over the top of the units to disrupt general auditory cues, T-units were interchanged, but the maze pattern was kept constant except for the fact that the kinæsthetic sequence was broken by the short-cut. The true r 's between efficiency on Trials 17, 18, and 19 with the situation unchanged and Trials 20, 21, and 22 with it altered were, for errors .78; for time, .95. Deleting Trial 20 where emotional upset or distraction might have entered, the r 's were, for errors, .85; for time, .94. Deleting both Trial 20 and Trial 21 gave r 's of, for errors, .95; for time, 1.00.

These high intercorrelations indicate clearly that differences between individuals are not controlled by sensory stimuli or responses conditioned to them, but apparently by the degree to which the animals have formed higher generalized distance-direction behavior-sets in the given situation.

An analogous experiment by Tolman and Honzik⁽³⁶⁾ sheds light on the psychological nature of the motive for maze learning. They ran rats 11 trials through a modi-

fied Stone maze, giving them *no food* at the end of the maze. Here, differences between rats could not be assigned to differences in reward-value of the food-goal, since it was absent. Then, the rats ran 11 more trials with food in the end-box—the typical maze procedure. The r for errors* between the two periods was .67, true .73. Thus, under two quite different sets of motivational conditions, the rank orders in ability were fairly similar. The cause may have been either a drive common to the two periods, say, the drive to get out of the maze proper (amplified by food in the reward situation), or differential capacity to cognize the spatial relations of the maze whatever the motive.

(5). *Evidence from the intercorrelation of different behavior-domains.* The validity and significance of a given behavior-domain hinges upon the way in which it is defined and measured and upon its importance to the species being measured. The correlation of this domain with other “outside criteria” may or may not divulge the psychological nature of the domain. What such inter- r ’s actually show is the *generality* of individual differences.†

To ascertain whether the inherited differences that appeared on Maze X were general characteristics of the rats

* Not reported by the experimenters, but obtained by the writer from them. Another group of animals that had the reward trials first and non-reward trials last gave an r of .67, true .71.

† In addition to this *objective* interpretation, such inter- r ’s can be analyzed into “underlying factors” by the mathematical methods of Spearman, Kelley, Thurstone, and others. These methods attempt to deduce general, group, and specific factors that are statistically consistent with the observed inter- r ’s. Though important analytical devices which deserve a prominent part in a systematic treatment of individual differences, these methods have not as yet been used in any problem dealing with subhuman animals, and hence they will not be considered here. Because of the possibility of rigorous experimental control of disturbing irrelevant factors in the case of animals, animal material is excellent for studies in factor-analysis, and doubtless many studies of this type will shortly appear.

Note. Shortly after the above was written, the mail brought the first published paper on factor-analysis in animals: Dunlap, J. W., “The Organization of Learning and Other Traits in Chickens,” *Comparative Psychology Monographs*, 1933, Vol. 9, No. 4.

that could be also observed in other T-mazes, the writer ⁽⁴³⁾ ran 141 animals on another 20-blind maze, Maze Y, and found the raw inter- r to be .77 (true .79) for errors on total trials. Even the errors on 3 trials on one maze, when correlated with total errors on the other, gave a true r of .91. This indicates a fairly general learning ability in two such T-maze domains. Other experimenters have found lower values. The Stanford workers, Commins, McNemar, and Stone, ⁽³⁾ report the results on 256 inbred rats who ran 40 trials on a 12-blind floor maze and 20 trials each on two elevated mazes, one with 12 blinds and the other with 20 blinds. The true r 's (for total errors) between the floor maze and the two elevated mazes were .65 and .56, respectively; between the two elevated mazes, the true r was .66. Miles ran 38 heterogeneous rats on two 15-blind T-mazes of the same pattern, one an alley maze and the other elevated, and obtained a raw r of .50 (true .59) for errors and one of .67 for time. ⁽¹⁸⁾ Leeper ran 34 inbred rats 30 trials on a modified Stone maze, waited an interval of 40 days, and then ran them on the mirror image of the maze for 20 trials. The raw r 's were .71 (true .76) for errors and .35 (true .40) for time. ⁽¹³⁾ Finally, Alm reports a raw r of .52 for total distance travelled in two simple 2-blind mazes and one of .57 for time. ⁽¹⁾ Since the reliability coefficients were above .90, the true r 's would not be much higher. Thus, it appears that between maze-learning domains, the coefficients for errors range from about .50 to .91. Studies should be made to determine the reason for these differences in values.

An entirely different picture is presented by the relationship between maze learning and other learning domains, such as problem-box and sensory sign learning. The Stanford experimenters reported for different groups zero r 's between time on the triple-problem box and errors on the T-maze. And between learning in the light-dark discrimination box and in the maze, the r 's were also zero—a fact

corroborated by Williams.⁽⁵²⁾ All of these measures had high reliability coefficients. The Stanford experimenters discovered zero correlations between sensory sign learning and problem-box learning. These facts are illuminating, for they point to the conclusion that the learning behaviors in these different situations are quite different kinds of learning—that there is no such fact as *general* learning ability, but rather that there are *numerous learning abilities*.

Another investigated relationship is that between activity and maze learning. Is the better learner also the more active and energetic one? Shirley ran two groups of rats in activity cages and then through an 8-blind maze.⁽²⁷⁾ Even though the reliability coefficients of both measures were high, the *r*'s between activity and maze errors and time were very low, giving little support to a postulation of such a marked relationship.

It thus appears that the intercorrelations between such a domain as maze learning and other domains shed little light upon the psychological nature of individual differences in maze learning. Behavior differences seem to be so specifically tied up to the unique situation in which they are measured that analysis should be confined to behavior *in situ*. One study that seems to be an exception is that by Krechevsky on "hypothesis formation" in rats.⁽¹²⁾ He ran the animals in a light-dark discrimination box, which was made unsolvable for the animal by sometimes having the light alley a blind and sometimes a true path, and by changing the dark alley likewise. The results showed that the animals tended to fall into two groups, those which followed one or the other of the visual cues *consistently*, acting as if it were the proper solution (these rats were classed as having *visual* "hypotheses"), and another group that formed right or left position-habits, disregarding the visual cues (these were classed as rats with spatial or kinæsthetic "hypotheses"). The animals used were 23 bright and 23 dull rats from

the writer's inheritance groups, and 80 "stock" rats. Krechevsky reports that the maze-bright animals tended to be kinæsthetic animals, whereas the dulls were preponderantly visual; the "stock" animals were evenly distributed into the two classes. The results of this experiment imply a high positive correlation between propensity for kinæsthetic "hypotheses" and maze ability. However intriguing are the possibilities of such relationships, the results must be checked by running not only, as here, the extremes in maze ability, but rats of all gradations in ability; also, the actual correlations should be worked. If under such conditions the r 's were high, we would have evidence as to some of the psychological determinants of maze ability.

High specificity of performance indicates that psychological analysis of individual performance can best be gained by a study of variables apparent in the situation proper. Correlations with "outside criteria" apparently are of little value. One fruitful approach to analysis is that in which controlled systematic variations in the situation or subjects are introduced, as is illustrated in section (4) above. Another approach is the one in which the experimenter does not attempt to control many variables that might affect individual performance, but lets them vary in the situation, measures them, and attempts to predict performance from them. Hall's work ⁽⁷⁾ indicates the fruitfulness of this approach. He let rats move at will in an open laboratory field which contained food enclosed in a barrier in the middle. He then tabulated, for each animal, distance travelled, amount of fæces and amount of urine eliminated, weight before and after regular feeding, amount of food eaten, and age, and discovered that certain movements of the rat in the field during some periods correlated (multiple) with a composite of these variables as high as .78. He thus uncovered certain important variables associated with activity of this type.

Conclusion and Prospectus

Comparative psychologists have made the beginning of a systematic attack on the problems of individual differences. While their work has been confined to the rat, the results lead to certain tentative conclusions: (1) In a given domain of behavior, wide and consistent individual differences exist, and in some behavior domains these differences persist throughout a considerable portion of life. (2) These behavior differences are quite unrelated to obvious morphological differences, and their physiological correlates are as yet unknown. (3) In certain domains of maze learning and activity, these differences are markedly determined by hereditary factors. (4) Ability seems to be highly specific: whereas it is consistent and constant in a *given* situation, between quite *different* situations (even though the behaviors in the two are similarly defined—for example, as “learning”) it appears to be highly variable. (5) The most promising approaches to an understanding of the psychological nature of the causes of individual differences are (a) a thorough *a priori* analysis of the situation in which the behavior is manifest, (b) a study of individual differences during a period in which the situation remains unchanged except for systematic variation of stimulus features, and (c) a study of the interrelation between sundry behavior variables *in situ*.

The contents of the preceding pages indicate that the scientific study of individual differences is characterized more by the prospects of future work than by a significant collection of conclusive data. Studies have been made only on the rat (and man)—and investigation of the rest of the phylogenetic scale still lies before us. In the rat, the major problems of individual differences have been attached only in the domains of maze learning and activity, and the many other gross domains of behavior (sense acuities, insight-

formations, delayed responses, simple conditioned responses, and so forth) remain relatively unexplored. As a consequence, our conclusions are really little better than speculations. We grievously need more complete studies on more behavior-domains in many more species.

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CHAPTER XIV

Social Psychology of Animals

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Introduction

THE preceding chapters have been devoted largely to comparative study of the capacities and modes of response of individual organisms as such. In the following pages, we shall consider behavior which involves more than one organism. The behavior of one or more organisms that affects or is affected by the activities of one or more other organisms is *social behavior*. By this broad definition, social behavior includes nearly all activities pertaining to reproduction and the rearing of young, nest- or home-building, defensive responses, grooming, communication, play, and the like. On the socio-psychological side, interest is directed to animal organizations from the relatively simple *associations*, which represent animals congregating because of their responses to common environmental factors, to the highly complex *states* typical of various insects and in which there are highly specialized castes and relatively permanent *communities*, which frequently are composed of many subgroups. We shall first consider social grouping and organization among animals, and from these turn to a consideration of different forms of social behavior as they occur at various phyletic levels.

Social Grouping and Organization

We might approach social organization in animals from the sociological standpoint, describing and classifying the various and variable forms of society, association, and state found among them, as done by Alverdes ⁽²⁾ and others. Zucker-
man ⁽²¹⁾ has classified the unions of mammals according to the underlying physiological mechanisms, principally those causing differences in sexual periodicity, which are responsible for the mutual attraction of their members. The subject has been approached from the standpoint of physiological ecology by Allee, ⁽¹⁾ and though he has been concerned largely with the effects of crowding upon various simple organisms, he has discovered principles which he believes explain the origins of social relationships. Each of these approaches to the problem has been profitable, but each has its limitations. The first, though highly inclusive, suffers from being largely descriptive. The second and third, though explanatory, cover only limited aspects of the problem. Activities associated with reproduction are among the most potent determiners of social grouping, but food-getting, self-protection, and many other forms of self-preservational behavior, including responses to the physical environment, contribute to the nature and permanency of social groups. A complete survey of the subject would require both descriptive and explanatory approaches in which all of these factors would be considered. In our brief consideration of social grouping and organization, we shall limit ourselves largely to the groupings that grow out of reproductive relationships. We shall bear in mind, however, that these social units commonly are but parts of larger and more complex social groupings.

"Solitary" animals.—Solitariness, as applied to social behavior, is a relative term used to designate limited social relationships rather than complete isolation of individuals.

At the lower phyletic levels, such as the single-celled protozoa and some of the metazoa, reproduction occurs through the division of the parent cell by processes of fission or budding. In some paramecia, small, slipper-shaped protozoa, reproduction by fission is at times preceded by conjugation. In this process, two paramecia come together and for a time remain attached to each other because of the adhesive state of their oral surfaces. Later, each of the conjugants divides into two daughter-cells, which, in the course of time, will themselves divide. Outside of this occasional conjugal relationship, these animalcules have no observable social behavior. Among many of the coelenterates, shellfish, and fishes, eggs or sperm-cells are emitted into the water by the females or males without regard to the presence or absence of the other sex. In these cases, fertilization of the eggs occurs by chance meeting of sperm and eggs. Many of the fishes come together at spawning time to emit their eggs and sperm in a common locality. Among birds, some cuckoos in most respects are solitary animals. The males take up their habitat in different localities. The females fly from one to another of them at mating time and then lay their eggs in the nests of other birds, where they are hatched and the young are reared by foster parents. There are frequently reported cases of solitary males among the higher vertebrates such as elephants and apes, which ordinarily live in groups. These physically and socially isolated animals, however, generally are believed to be individuals who because of age or physical incapacity have been driven from their original group by more vigorous males. Their behavior does not typify the general social life of their species.

The animals mentioned above may be regarded as socially solitary. This does not mean that they necessarily live isolated one from another. Even the single-celled paramecia gather about bits of decaying vegetable matter, where they are held in large numbers by their positive reactions

to the acids of decomposition. In the same manner, when a group of them come together by chance, they are held temporarily and their number is increased by the reaction of others to the CO_2 given off by the bodies of the group. Others of the solitary animals, such as many of the fishes, move about or feed in large groups, or gather in certain localities at spawning time, though without actual meeting of the sexes for purposes of reproduction. In the relatively solitary animals, such as the cuckoos previously mentioned, aside from mating there are no social bonds between the two sexes, members of the same sex do not associate with each other, and no social contacts are made between parents and young.

Mateships.—In contrast to the sexual promiscuity and social isolation of the solitary animals are the animal mateships that are formed between members of the opposite sexes because of sexual attraction. Mateships vary in three different respects: (1) they may be *temporary*, lasting only through a given mating season, or they may have varying degrees of *permanency*, enduring for several mating seasons or throughout the life of the given individuals after the first mating; (2) they vary in the numerical representation of the two sexes within the mateship as follows: (a) one male and one female (*monogamy*), (b) one male and two or more females (*polygyny*), (c) one female and two or more males (*polyandry*), and (d) two or more of both sexes (*group mateships*); (3) they also may be classified by their isolation from larger groups (*solitary mateships*) or by their inclusion as a unit within a community (*intra-group mateships*).

It is impossible within the limits of this chapter to give examples of more than a few of the numerous categories into which mateships fall as a result of the various permutations and combinations of the factors enumerated above. For further examples and for references to literature on the subject, the readers are referred to the work of Alverdes.⁽²⁾

Temporary mateships.—Temporary monogamous mateships are known to occur among many fishes and birds and among some mammals, such as foxes, wolves, and bears. The female salmon lays its eggs and they are fertilized by a single male, which remains present while they are being laid. Foxes, wolves, and bears live in pairs both during rutting season and for a time afterward, the male fox at times contributing to the care of the young. The mateships of the three last-named animals are solitary, though in the case of wolves, the separated members of various mateships gather in packs during the winter months.

Many of the ungulates, such as the Indian buffalo, elk, and some wild sheep and goats, unite in polygynous mateships during the rutting season. The organization of these social units usually arises through the aggressiveness of a physically dominant male who drives the weaker males away and assumes leadership over the remaining harem of females. Among the animals just mentioned, the formation of the polygynous mateships results temporarily in the breaking up of the herd formations that exist outside of the mating season.

Permanent mateships.—Permanent, solitary monogamous unions are known to be typical of eagles and hawks, and they also occur among some of the migrating birds, such as the robin, in which the members of a pair either migrate together or find each other at the end of migration. It is believed that seagulls, ravens, starlings, herons, and some ducks, which are gregarious throughout the year, are united in relatively permanent pairs. Whitman ⁽¹⁷⁾ has shown that this form of mateship frequently occurs with the domestic pigeon. These birds divide into pairs within the flock. Once mated, the females commonly are faithful, though the males occasionally accept other females.

Relatively permanent polygynous mateships are common. In large groups of domestic fowls, there is a tendency for a cock to take unto himself a number of females, defending

them from the attentions of other cocks. The same tendency is shown by horses on the western plains of the United States, where a stallion leads his own band of mares. A female accidentally separated from its group, however, is usually accepted without opposition by the male leading another group. Among apes and monkeys, as will be shown in greater detail later, present evidence is conflicting concerning the most common forms of social grouping. In many of these animals, polygynous mateships are known to occur, though under some conditions it is probable that monogamous unions and promiscuity exist.

Polyandrous mateships appear to be rare. In the worm *Bonellia*, as many as eighteen of the small-sized males attach themselves to one of the relatively large females. In certain spiders, each of the females has two males with which it copulates. Females of the crab *Alcippe* have from three to twelve small male mates, which remain with them throughout life. In so far as it has been observed in the animal world, polyandry seems to be associated with great disparity of size (the females being larger), and with a predominance in the number of males.

Families.—Family groups vary according to the relationship of the parents to each other and of the offspring to either or both of them. Among forms where there is asexual reproduction, among solitary forms where the eggs are laid separately and left to hatch unattended, and among many of the marine forms where eggs and sperm are deposited at random in the water, family groupings do not occur. The simplest family unit is the *child family*, in which offspring of similar age unite and remain together for variable periods of time. The young of some caterpillars and of some of the fishes group together in this manner. In some fishes—the stickleback, for example—the male builds a nest and leads several females to deposit their eggs in it, where he fertilizes them. He watches over the eggs until they hatch and then guards the young for a time. The family group

thus formed may be regarded as a *father family*. More common in the animal world are *mother families*, in which the mother alone assumes the care of the young. This form of family occurs among many insects, such as spiders and scorpions, and is prevalent throughout the vertebrates. Most complex and most important psychologically are the *parent families*, in which both male and female parents participate in the care and the protection of the young. This type of family is common among polygynous animals, where the contribution of the male parent to the welfare of the young usually consists of little more than protection. Its most interesting form, however, occurs in monogamous mateships, such as those among many birds, where such parental responsibilities as the building of the nest, sitting on the eggs, and feeding the young are shared equally by male and female parent.

Herds and communities.—Consideration of the principal forms of social groupings among animals is not complete without mention of the larger units, namely: herds and communities. We already have seen how paramecia collect in areas where acid concentration is high. Many fishes move in large schools even at other periods than spawning ones; several of the ungulates run in large herds but break up into polygynous mateships at rutting time; carnivores, such as wolves, live in packs during the winter but pair off for mating in the spring; and numerous birds, such as sea-gulls, ravens, and starlings, form monogamous mateships, though they live gregariously—sometimes in enormous flocks.

Somewhat different are those communities formed by animals that construct relatively permanent abodes. An example of these is to be found in the case of the prairie dog communities on the western plains of the United States. Many families of these rodents construct elaborate underground burrows, frequently with connecting corridors. The writer has many times observed the interdependence of the

family groups forming such communities. If a human being approaches a prairie dog town, a warning cry is given by the first individual who observes the danger. At once the cry is taken up by certain other individuals throughout the community. All of the animals near the approaching source of danger scurry to their burrows, only sentinels remaining upright on their haunches on the entrance mounds. At the last moment, these make quick, chirruping sounds, flop their tails rapidly, and then drop from view. The progress of an observer passing through a large community is marked by a regular wave of the small, squirrel-like animals as they rush into their burrows. Before he has gone far, however, loudly screaming sentinels appear behind him. These are soon followed by other members of their families. Within a few minutes after the observer has passed beyond the community, all members of it have come to the surface again and, with the exception of the sentinels which are still on duty, are nibbling at grass and roots, basking in the sun, or playfully romping with each other.

These large aggregations of individuals vary in the nature of their organization from mere collections of socially solitary animals to colonies made up of families arising from common parentage or formed by the association of unrelated families in a single group. They may be temporary, as in the case of birds that unite in flocks for migration or of wolves that run in packs during the winter, or permanent, as in the case of beavers or the prairie dogs just described.

Factors Determining Social Relationships

In the preceding account of the principal social groupings among animals, little indication was given of the causative factors involved. With individual behavior still so incompletely understood, it is impossible fully to explain the

extremely complex behavioral relationships between individuals or groups. For the most part, the same factors which determine the behavior of a single organism must be looked to for explanation of the organism's behavior in relations with other organisms. Animal organisms must adapt to each other and to their *physical environment* so as to secure food and to insure protection from the elements and from their enemies, or they perish. The degree and manner of their adaptation are determined by their *structure*, their *physiological equipment*, and their *psychological tendencies*. These factors will be considered in the order stated.

Physical environment.—Animals may be thrown together because of their common response to factors in their physical environment. This is the case where certain protozoa that react negatively to light (negative phototropism) collect in shadows, or where animals gather in groups about water holes or sources of food. The eggs and sperm of aquatic and amphibious forms that would soon degenerate if exposed to air are preserved for a time, after which they are secreted in water. This makes the meeting of the opposite sexes, which is essential for reproduction in land forms, unnecessary in these organisms. Prairie dogs furnish a splendid example of the effects of physical environment upon social grouping. Hollister ⁽⁶⁾ has shown that on level ground where grass and roots are plentiful their villages sometimes extend for several miles, while in rough areas unsuited to sustain large numbers of the animals they necessarily live in widely separated pairs or families. In northern regions or at high altitudes where winters are severe, these animals hibernate during bad weather; while in the lower central plains, they come out on all pleasant days throughout the year.

Rough and broken terrain commonly limits the size of social groups; climatic changes affect migration and hibernation; the prevalence or nature of available food influ-

ences food-getting habits and determines whether the food shall be sought by individuals or by groups and whether by small or large groups. In such ways as these, environment directly or indirectly serves as a determinant of social relationship.

Structure.—Structure and function are so closely associated that commonly their individual effects cannot be distinguished. The specialized structure of the mountain goat enables him to inhabit areas where few other animals would survive; and the nature of this territory in turn affects the type of social grouping of this species of animal. We have seen above how size is apparently one determinant of polyandrous unions. The extremely complex social organization of the social ants, bees, wasps, and termites affords splendid examples of effects of morphology upon social relationships. In the social ants, for example, there are egg-laying queens, males, and sterile females, or workers, of various types. In these polymorphous species, each class is specially equipped structurally to perform certain types of activity in a highly complex social state. It also should be remembered that the sensory modalities that so largely determine the behavioral capacity and adaptability of individual organisms are dependent upon appropriate structure.

Physiology.—Among all animals, except those lower forms that reproduce asexually, sexual periodicity is an important determinant of social relationship. Many insects have a life span of but a single year and mate but once. The males of some species of ants die immediately after mating, though the egg-laying queens have been known to live for as long as ten to fifteen years, during which time they remain fertile as a result of the initial fecundation. Fish commonly have an annual spawning time. Among mammals, with a few exceptions, the females experience recurrent periods of œstrus (sexual receptivity), separated by anœstrus intervals, when they are non-receptive. In ani-

mals whose œstrus recurs at frequent intervals, for example, at intervals of four to five days in the rat, four to five weeks in the baboon and chimpanzee, and approximately ten weeks in the dog, the sexual apparatus of the male is continuously functional. Where, however, there is an annual rutting season, as is the case with ferrets and most deer, the sexual functions of both male and female are usually quiescent during the intervening periods. The mutual attractiveness between the sexes thus is determined largely by their physiological mechanisms.

Other physiological factors determine in whole or in part the nutritional needs of the organism, the relation of offspring to parent, the nature and degree of protection from the elements necessary, and the ability of the individual or group to protect itself from enemies.

Psychological factors.—Emotions play an important part in social organization. Fear may draw animals together for protection from a common enemy, while anger, frequently infectious, may lead to mass attack upon a foe. Emotional factors enter into the behavior of a dominant male when he drives other mature males away from his females, thereby determining the polygynous nature of his family group. The role of affectivity in play and sexual activities of birds and mammals is an example of numerous social activities in which the emotions play a part.

The tendency of one animal to change its behavior to conform to that of another also contributes to the cohesiveness of groups. Commonly, a group of animals, all engaged in a single activity, will immediately follow the example of the first one of their number who turns to another activity. It is said of herds of cattle that if one eats they all eat, and if one drinks they all drink, and one often justified explanation is that they are responding to a common stimulus. But one sheep in a quietly feeding herd may become startled and throw all of the others into a panic. When one member of a group of grazing cows saunters

across the road, the others commonly follow. In these cases, the initiator of the new activity is responding to a different stimulus than are those which follow him. The group of sheep may respond because of the spreading of the initiator's excitement, but no such element is observable in the case of the cows. Nor can behavior of this type be attributed to "gregariousness," for the tendency to congregate would hold the majority together rather than permit them to trail after one individual.

The fact that some organisms at the same phyletic levels lead solitary lives while others are social raises the question of whether these opposed tendencies are inherited or acquired. Among solitary animals, whose eggs are laid separately, the young, left to shift for themselves, tend to follow a socially solitary existence. Young hatched from deposits of eggs, though without parental care, commonly form temporary child families. The young of most mammals, which are relatively helpless at birth, and which therefore experience prolonged periods of dependence upon parental sources of nourishment and protection, learn to make social adaptations: they form habits of behaving with and in conformity to the behavior of their parents and other animals of their kind. Though physiological and morphological factors to a large extent determine the nature and extent of this early child-parent relationship, psychological factors—the social habits formed during infancy and childhood—largely determine the nature and extent of the social tendencies that persevere following childhood. Gregariousness, the tendency to congregate, is largely the result of early-formed social habits rather than of inherited tendencies. The social animal develops habits that are incongruous when it is isolated. These habits lead it to seek the companionship of others of its kind toward which this habitual social behavior may be directed.

Is there evolutionary sequence in the nature of social groupings?—When studying any common aspect of animal

behavior in which there are varying degrees of complexity, one naturally looks for evidence of some sort of evolutionary sequence. Thus, one might expect to find the simpler social orders among the more primitive organisms, with an increase in complexity as the phyletic scale is ascended. In our present study, such expectations are fulfilled to but a slight degree. Complete social solitariness occurs only in some of the lowest animal forms. On the other hand, among insects of the same order, there occur both the solitary forms in which individuals come together only at mating time and in which there is no familial organization, and the social forms with societies second only to man's in complexity. Similar variability is found among birds. The parent families among many species of birds greatly exceed in complexity the familial groupings of most mammals; while at the other extreme, the so-called parasitic forms, such as the cuckoo, live what is essentially a solitary existence. Several factors are responsible for this general situation. Taxonomic classification is based upon relatively rigid and invariable structural differences. On the other hand, social organization, while partially determined by structure, is largely the result of behavioral and physiological adaptation to highly variable environmental influences. This fact explains why different breeding habits may occur in animals of the same order, while animals of widely divergent orders may have the same breeding habits. It also explains why there is so little correlation between the complexity of social organization in a given form and the position of the given form in the phyletic scale.

The Social Life of Insects

The majority of insects are socially solitary to the extent that the sexes come together only for purposes of mating. The females commonly lay their eggs and then go on their way, leaving their young to shift for themselves. In some

forms, however, as the Peckhams have shown to be the case with the solitary wasp,⁽⁹⁾ the females make elaborate provision for the welfare of their young. They make holes in wood, dig tunnels in the earth, or build nests of mud in which to lay their eggs. The nests are then provisioned with larvæ or other insect forms, which serve as food for the young when they hatch.

Quite in contrast to these simple social relationships, and to most of the others we so far have considered, are the highly complex colonial relationships that exist among social ants, bees, wasps, and termites. In each of these insects, there are highly specialized structural and functional differences separating them into egg-laying queens, males which serve only to fertilize the young females, and sexually undeveloped females, workers, which carry on the activities necessary to provide food, shelter, and protection for the colony and the essential care for the young. An idea of the complexity of the social organizations of these insects may be gained from descriptions of the formation of ant colonies by Wheeler.⁽¹⁶⁾

Among some species of ants, when the breeding season arrives, the young males and females from colonies in the same neighborhood come to the surface of the ground for the first time on the same day or even at the same hour. After running about for a time, they spread their wings and fly high into the air. During this, their nuptial flight, the male meets and fecundates the female, and then descends to earth to die soon after.

When the female descends, she detaches her wings and then digs a small chamber in the earth. She enters and closes the opening. In the course of weeks or even months, eggs fertilized by the sperm stored within her body during the nuptial flight are laid. From the eggs hatch minute larvæ, which she feeds with a salivary secretion. The larvæ develop into pupæ and eventually come forth as small but otherwise normal workers. These workers soon take

entire charge of both the nest and the queen. They bring in food. They build a larger nest, if necessary, constructing it in a more suitable location. They may carry water to moisten the soil in which they dig their home. The queen, well fed and properly groomed by the workers, soon lays more eggs. The workers care for these, and later act as nursemaids to the larvæ.

In addition to the domestic activities we have mentioned above, the workers engage in other highly specialized forms of behavior. Some species of ants adopt aphids (plant lice), from which they secure sweet excrements. Numerous instances have been reported where the workers collected aphid eggs, cared for them through the winter, and in the spring placed the newly hatched aphids out to pasture on the stems and roots of plants. Certain workers of the leaf-cutter ants cut out pieces of leaves and carry them to their nests, where other workers pack them into balls on which they cultivate a fungus which serves as food for the colony. In some species, the workers are differentiated into large, medium-sized, and small workers and soldiers, each form of which carries on its own duties.

With the strict division of labor between queen and various types of workers, the ant colony develops from the original fecundated, egg-laying queen into a highly complex social organization numbering from a few dozen to several thousand individuals. From a reproductive standpoint, the ant colony may be regarded as a mother family, made up of the queen and her offspring, all functioning to preserve the original household as well as to provide further queens and males for the establishment of new ant colonies.

The Social Life of Apes and Monkeys

Apes and monkeys, in contrast to the relatively simple insects we have just considered, represent the two highest types of animal development next to man. With their

dextrous fingers and toes, their acute sensory organs, and their highly developed neuromuscular equipment, these subhuman primates potentially are endowed for social behavior of far greater complexity than that of animals at any of the lower phyletic levels. These facts have long been recognized, and as a result, the behavior of the subhuman primates has received much attention. Until recent years, however, most of the information concerning them has consisted of anecdotes or mere fragmentary reports of hunters or explorers. During the past decade, the extensive literature relating to them has been collected and evaluated,^(19,21) and the study of their behavior has gone forward at a pace unparalleled in the case of any other animal form.

Laboratory investigations already reported and many others still under way prove that the chimpanzee and the macaque monkey, respectively the representatives of the great apes and of the Old World monkeys thus far most studied, must be regarded as falling into two widely separated behavioral levels. Though these two animals bear close resemblance to each other both structurally and physiologically, chimpanzee behavior more nearly approaches man's than does the macaque's. While study of the social behavior of these animals has only been begun, there is sufficient evidence at hand to indicate the general nature of this behavior.

Group organization.—The size and nature of social groups formed by apes and monkeys are variously reported for different species as well as for the same species. Many forms of Old World monkeys run in large bands, frequently numbering fifty or more, and again are found in small groups that may consist of but a single family. Dr. Ray Carpenter, in a recent and still unpublished study of the howler monkey *Alouatta palliata*, found this species in bands of *from 3 to 35* individuals. Females represented between 60 and 70 per cent of the total adult population. Gorillas have usually been found in groups of eight or ten

individuals. Chimpanzee groups observed by Nissen ⁽⁸⁾ varied in number from 4 to 14, and many of these groups contained more than one mature member of each sex. Approximately half of the members of each group were small, probably immature, animals. Yerkes and Yerkes find evidence in the literature in this field that the orang-utan tends toward solitariness and also toward segregation of the sexes. All of the other forms of great ape, the siamang, gibbon, chimpanzee, and gorilla, these authors believe, live in bands or herds, the chimpanzee and gorilla bands being made up of family groups.

Zuckerman, ⁽²¹⁾ on the basis of the literature in this field and of his study of baboons, decides that most wild primates are polygynous. According to his view, the social unit among the subhuman primates is the harem. Among the baboons he observed on Monkey Hill, in the London Zoölogical Garden, the harem consisted of an overlord, or dominant male, his females and their offspring, and bachelor males who attached themselves to the family party. The overlord maintained his position of dominance through his physical supremacy, and once he was vanquished by the younger males, he reverted to the socially inferior position of the bachelors. Interpretation of these observations of the baboon necessitates consideration of the fact that though the animals were turned loose upon an artificial island and were in a semiwild state, there were originally over ninety males to only six females, a sex ratio quite different from that usually found in the wilds. That changes in the social grouping and social behavior of these animals would have occurred with different ratios between the sexes seems probable.

As was described in the case of prairie dogs, environmental factors greatly affect social organization. Among animals whose behavior is as complex and as variable as that of monkeys and apes, the nature of their social groupings will be greatly modified by their physical surroundings.

We may expect to find great inter- and intra-species differences in familial relationships as well as in the larger social groupings of these animals. In territories where suitable food is scarce or where the terrain is unsuited to the life of these animals, the size of groups would be reduced to either polygynous or monogamous families.

The sexual behavior of the female ape or monkey, of the species so far studied, is usually almost entirely passive. She demonstrates sexual receptivity by taking a presentation position before a male. It seems improbable that in a band of several dozen active monkeys a dominant male could keep his particular group of females segregated and protected from the attentions of other males. In such cases, sexual promiscuity is probably the rule.

The many apparently conflicting observations upon the social life and the social organization of the various forms of subhuman primates indicate neither errors of observation nor errors of report. Instead, they point to the great behavioral flexibility that is to be found in highly adaptable animals existing under various environmental conditions. Polygyny and sexual promiscuity are reported most often. Monogamy is less often observed, and polyandry can be expected to occur only under very special conditions, if at all.

Behavior and maternal care of the young.—The mother-child relationship in animals shows about as little approach to an evolutionary sequence as do other forms of social behavior. The females of certain marine forms guard their eggs and protect their young, while those of other similar forms lay their eggs and then desert them. Similar differences in maternal behavior are observed among insects. In contrast to the parental care bestowed upon their young by most birds, some species of the cuckoo and the American cowbird shirk all maternal responsibilities by laying their eggs in the nests of other birds, where the eggs are hatched and the young are reared by foster mothers. Among mammals, there are great differences in both the nature and

the duration of the care bestowed by mothers upon their offspring, these differences apparently being determined largely by the degree of helplessness of the young and by the time it takes them to become independent. Among the subhuman primates, with which we are primarily concerned here, only the chimpanzee and the macaque monkey (*M. mulatta*) have been studied to any extent.

The macaque is born after a gestation period of approximately six months.⁽¹¹⁾ Before his body has been fully expelled from the birth canal, he begins to be active. As his head is expelled, his eyes begin to blink and his mouth opens and closes. When his shoulders and arms are freed, he reaches out with his hands and grasps any object with which he can make contact, whether this be the floor or wall of his cage, or the body of his mother. This first grasping response is exceedingly important, for monkey babies are born in the crotches of trees, and occasionally in the process of birth there arise complications that would result in their falling to certain death on the ground below if they did not support themselves momentarily by clinging to the nearest branch. Chimpanzee babies, the writer has observed, appear less active immediately after delivery. The chimpanzee, like the monkey, shows the initial grasping tendency at birth; but this infant, born after a gestation period of nearly nine lunar months, is far weaker physically than the monkey baby, and it cannot support itself in the same manner unaided. Immediate grasping is not so essential for the chimpanzee, however, for it apparently is born in a nest such as these animals construct to sleep in, and therefore there is slight danger of its falling to the ground after delivery.

Immediately after delivery, the monkey mother holds the baby while she carefully licks from its body the fetal fluids with which it is covered. This licking is done by the mother not in an effort to cleanse the baby, but rather because at this time she has a particular craving for these

fluids. Once the fetal fluids are removed, the grasping reaction of the baby again becomes important. The mother typically holds the baby either over one arm or against her breast. But she does nothing to determine the orientation of the infant relative to herself. By its grasping reaction, the baby turns itself so that its ventral surface is toward the mother's breast, and in this position it discovers the nipple unaided. If the baby, because of prematurity or other reasons, is too weak thus to orient itself in relation to its mother, the latter does nothing to facilitate its receiving nourishment, and it perishes.

Though the normal monkey baby may be strong enough to stand or even to walk a little within a few hours after birth, it usually spends all of its early days of infancy at its mother's breast. During the first two weeks, it begins to survey its environment visually. Shortly thereafter, it begins to reach out in attempts to touch objects, and it tries to seize food which the mother is eating or which lies upon the floor of the cage. The mothers typically try to prevent this behavior, though they welcome the suckling of their young. The relationship between the chimpanzee baby and its mother is determined in much the same manner, though this baby is less active at birth than the monkey, and its physical behavioral development is much slower. When either of these babies reaches the exploratory stage, maternal tuition begins.

There are two types of maternal tuition, one inhibitory and the other stimulatory or directive. The monkey mothers that Doctor Hartman and the author observed taught their babies only by inhibiting certain activities. The babies must not disengage their hands or feet while the mothers are moving about and they must not hang pendulantly under the mothers' breasts. If they do, the mothers may repeatedly draw them sharply into place, even cuffing them, if the first method fails. One mother, after failing with these methods, drew her baby tightly to her

and then repeatedly pitched up and down until the baby learned to cling tightly to her to avoid being dislodged. In similar ways, the babies are later taught not to wander far from the mother and not to approach strange objects.

The chimpanzee mothers teach their babies all of these things and in much the same manner, but in some cases they have been known to employ directive methods of tuition also. One of the chimpanzee babies the author observed was born prematurely and was retarded in its physical development. At fourteen weeks of age, it was still small and relatively weak and had shown no interest in walking. During the fifteenth week, the mother was observed as she spread a burlap bag on the floor of the cage and then placed her baby upon it. She then withdrew two or three feet, seized one corner of the bag and drew it toward her. This seemingly failed to accomplish her purpose, for she next approached the baby, held it in her hands, and moved it along with its feet barely touching the floor. At other times, she repeated the process with the baby supported on her outspread hand resting under its belly. Gradually, the baby began to move its feet along the floor as if it were walking. Later, the mother withdrew one or two yards from the infant and then by repeatedly bowing and gesturing with her hands, she urged it to come toward her. At times during this process, she reached out and drew the baby forward an inch or two. Whether the baby would have learned to walk at this time without maternal tuition cannot be said, but there was evidence that the mother's behavior was directive and encouraged her infant in its efforts.

Macaque babies remain dependent upon their mothers for a year or more—in some cases, even after the mother has borne a later baby. Chimpanzee babies have a much longer period of infancy, and it is probable that they cling to their mothers during most of their first two years of life. During this period of infancy, the ape and monkey

babies gradually become more and more independent physically; but at the same time, they learn to adapt their behavior to that of their mothers and their other cage mates. During this period, as we shall see, they are transformed from parasitic organisms, dependent upon their mothers for nourishment and protection, to physically independent individuals with well-established social habits that are appropriate only when they are in the company of other individuals of the same or of different species.

Other forms of social behavior.—Besides social organization and forms of social behavior that are associated largely with reproduction, there are social activities that develop largely from experience. The need of the lactating mother to be nursed and that of the infant for this source of nourishment and for maternal protection gradually disappear. As these physical and social requirements are met by the cessation of lactation and by the increasing strength and activity of the baby, their place is taken by other gradually appearing forms of dependence. From the day of its birth, the mother examines the body of her infant and picks through its fur, incidentally removing any foreign objects that she finds there. The body of the mother likewise becomes an object of interest to the baby. While the baby is still relatively weak and poorly coördinated, the mother begins to play with it, and soon it in turn begins to play with her. Activities such as these result in the development of social habits and companionship. Just as the mother, when an infant in the arms of her maternal parent, learned to adapt her behavior to that of another, so her baby in turn learns to adapt its activity to her. We shall now consider briefly play, grooming, and coöperative behavior, which have their beginnings in this early mother-child relationship.

Play.—The waking hours of animals are devoted to activity of one form or another. Among many animals, particularly the lower forms (and among all forms under

certain environmental conditions), behavior necessarily is devoted largely to food-getting, to securing shelter, and to reproductive activities. Among animals of the higher levels, these physical needs commonly are satisfied by the expenditure of but a portion of the organism's time and energy. In the case of the latter, the tendency to behave continues after physical needs have been met. The activities which occur under these conditions of surplus time and energy (the surplus-energy theory of Schiller and Spencer) and which are enjoyed purely for their own sake (see Groos⁽⁵⁾) constitute play.

The play of the chimpanzee is far more complex than that of the macaque, and that of the macaque, in turn, is on a far higher level than that of the domestic dog and cat. Racing, romping, play fighting, and wrestling are common to all of them. The cat is attracted by small moving objects and characteristically engages in batting them about with its paws and then chasing them. The dog likewise plays with objects, usually carrying them about in his mouth, sometimes throwing them and frequently biting them to pieces. The author has presented four tame and well-adapted macaques and four equally tractable chimpanzees with a simple cart made from a small board with two wheels attached to the axle by nuts placed outside of washers. Typically, the monkeys approached this toy, picked it up, smelled it, bit at it, revolved the wheels, and then tried to tear it to pieces by sheer force. The chimpanzee subjects did all of these things but in addition removed the nuts from the axle and then took off the wheels. Three of them went even further than this and, to varying extents, reassembled the cart. In this reconstruction, there was no order to the process. Washers, wheels, or nuts might be placed on the axle first, and in the end the cart usually was in a badly dismantled state. There are great individual differences in such behavior, and probably from a number of macaques or other species of monkeys, some in-

dividuals would be found who would to a certain extent duplicate the behavior of the chimpanzees. In general, however, while both macaques and chimpanzees tend to be destructive in their play, constructiveness, as demonstrated by the attempts to reassemble the parts of the cart, is more characteristic of the chimpanzee.

The example we have just given is one where but a single animal was involved. Similar, though less easily described, differences appear between the group play of chimpanzees and that of macaques. Köhler ⁽⁷⁾ has described group behavior in which several chimpanzees joined in forming a circle about a post and then walked or trotted around, each keeping time by stamping with one foot. Similarly, a group of chimpanzees may gather about a pile of wooden blocks and all participate in alternately heaping them up and scattering them about, much as several human infants would do, or three or four of the same animals may unite first in tearing down and then in demolishing a heavy wooden door or some equally cumbersome object to which they have access. When attacking or tormenting an animal, either macaques or chimpanzees commonly join forces; but chimpanzees frequently, macaques seldom, engage in complex play activities in which all members of a group join uniformly in the same general behavior. Chimpanzees, furthermore, demonstrate far more variability and inventiveness in their play.

Among young subhuman primates, play has definite biological value. Such animals exploit both their physical and their mental capacities in inventing and carrying out new activities. They run, jump, climb, wrestle, and play at fighting. They go through the pattern of sexual behavior which they will follow during adulthood, though the sex-play activities of the young are far more varied than the reproductive behavior patterns of the adults. Through these activities are developed coördination and skill, which serve practical ends in facilitating the food-getting, self-

protective, and reproductive activities of later life. Group play also enhances the social adaptability and the co-operativeness which are essential for group existence.

Coöperativeness.—Social life arises from the mutual interdependence of organisms with the resulting mutual aid or coöperation that occurs among them. After surveying both the harmful and the beneficial effects of crowding upon lower organisms, Allee ⁽¹⁾ concludes that mutual interdependence of a physiological nature exists among the lowest living organisms and must have its antecedents in non-living matter. He finds survival value even in the tropistically conditioned grouping of animalcules. Out of this original social mechanism, he traces the development of group as contrasted with individual responses and, finally, the closer coöperation that becomes possible with the development of the nervous system. In the subhuman primates, we have animals endowed with a neuromuscular system second only to man's. We shall consider the nature and extent of coöperation that is demonstrated in their behavior.

We have seen how ape and monkey mothers lick the fetal fluids from their newborn. But they do it because they relish these fluids. They welcome the nursing responses of their infants, although they object strenuously to their securing food from other sources. They cling to their babies and protect them from danger, though in a similar manner but to a lesser extent, they will fight to retain other cherished possessions, such as playthings.

Both young and old will rush to the protection of a member of their group, or will fight to prevent one of their number from being removed.

The young and adults alike indulge in hetero-grooming activities. They examine each other's skin for long periods at a time, removing the minutest foreign particles, bits of dead skin, splinters, festered hairs, or ectoparasites, if any are present. In a similar manner, one animal will examine

a wound of another, carefully picking away dirt, squeezing out and removing pus from an infected area, or pulling off scabs that have formed. Both examiner and subject seem to derive great pleasure from this activity, even though at times it may be painful to the subject. Yerkes ⁽¹⁸⁾ goes so far as to suggest that behavior of this type may be a forerunner of human hair and skin dressing, nursing, and medical and surgical treatment.

When it comes to sharing food or playthings, monkeys and apes are extremely selfish. The dominant animal of a group will commonly garner all food in sight, though he can consume but a portion of it. Young or weak animals may not be permitted to eat until the older or stronger ones have become satiated. At times, this situation is modified by bonds of friendship between a strong and a weak animal. In one pair of adolescent chimpanzees the author observed, the female, who was older, would at times share a delicacy, such as a banana, with the younger male, of whom she was extremely fond. This male, however, shared nothing. When a new play-object was introduced into the cage, he would assume command of it and continue to play with it as long as there was competition for its possession. If one of his cage mates, a stronger male, approached the object, even after he had tired of it, he would rush at this animal, strike or kick him, and then run away shrieking as if he had been molested seriously. The older female would then rush onto the scene, chastise the other male, and then stand guard while her friend resumed playing with the object.

Though, as has been described, these animals carefully and efficiently dress the wounds of their cage mates, this process does not necessarily indicate any special sympathy for the sick or wounded. A sick or wounded animal immediately loses caste in his group. Animals that he has dominated now dominate him or even abuse him, though

their reaction toward him may change immediately from abuse to careful grooming.

Instances have been observed where mothers have clung to the remains of their dead babies until, through decomposition and actual wear, these have been reduced to mere shreds of skin. But while one of these mothers would fight to retain the remnants of her offspring, she might at the same time move about bearing it roughly in one hand so that it thumped repeatedly against the floor or wall of the cage. If the remains of a baby are forcibly removed, the mother is distressed for only a short time.

The removal of an animal from a group by death or other causes brings forth various responses. If a young baby is taken from its mother and removed from sight and hearing, she remains disturbed for but a few hours after the separation is accomplished and two or three days later may show no evidence of recognizing her offspring. If the baby, though placed out of sight, is within the mother's hearing, she may sit for days staring toward the place where it is kept, continually calling to it. When one animal of a friendly pair which has long been caged together is removed, the remaining animal shows all evidences of loneliness. But if he immediately is given a new cage mate, he usually shows no signs of missing his former companion. A dead monkey may attract no attention from its cage mates, or they may collect about and pick through its fur. Zuckerman⁽²¹⁾ reports that the baboons he observed reacted socially to their dead companions as if the latter were alive but passive. From evidence such as this, he concludes that monkeys and apes do not recognize death.

Social behavior of the types we have just described show the subhuman primate to be primarily selfish. He seldom shares his food. His playthings are usually dominated by him exclusively. On the other hand, he engages in group activities in which he and his companions find mutual enjoyment. He cleanses his newborn and he grooms his com-

panions or dresses their wounds—and these are forms of behavior which contribute to their well-being. But he apparently does these things largely because of the personal satisfaction he derives from doing them. The behavior of the mother in protecting her infant from injury, the rushing of an individual or a group to the defense of a comrade, and the rare sharing of food may likewise each carry its own reward, though these rewards are relatively remote and unobjective, as are the rewards in much of the altruistic behavior of man. There is little evidence that the sub-human primates are purposively coöperative. They largely do what they are impelled to do because of habit or of satisfaction derived from the specific activity. The social behavior of these primates is originally, however, adaptive in nature, and much of it is beneficial both to the individual and to his fellows.

Communication in Animals

The mutual adaptation of animals that constitutes social behavior necessitates some form of individual or group expression recognized and responded to by other individuals of groups. This expression may consist of gross bodily movements, of gestures, of facial expressions, of sounds produced either vocally or by pounding or stamping, or of language in which certain vocal patterns have definite symbolic significance.

Social animals may be stimulated to run or fly by the running or flying of others, or by the outcries of the initiator of the activity. Von Frisch ⁽⁴⁾ has shown that honeybees, upon returning to their hive after discovering a plentiful supply of food, communicate the fact by executing rapid circus movements on the honeycomb. The bees near at hand then become greatly excited and set out in search of the supply. Practically all mammals indicate their emotional state by their general bodily posture, by the posi-

tion of their ears, by the expression of their faces, and, as is the case with many of them, by making sounds characteristic of certain affective states—particularly, anger. Here it should be pointed out that among most of the animals, the significance of these various forms of expression varies according to the particular situation in which they occur. The reclining ears, bared canine teeth, and growling sounds of an angry dog constitute a danger signal, though the same behavioral expressions may occur with an entirely different connotation during play or when the animal is demonstrating affection. Such expressions are seldom misinterpreted, however, for both animal associates and human observers respond, not to the expressions alone, but rather to the expressions as they occur in a given type of situation.

The author has had some opportunity to observe the development of various modes of communication between chimpanzee and monkey mothers and babies. The chimpanzee mother begins by expressing commands to her infant by physical force, when, for example, she draws it sharply down from a position about her neck to the more suitable place before her breast. At a later time, when she becomes disturbed by loud sounds or other unusual events when the baby is wandering away from her, she rushes to it, seizes it, and clasps it to her breast. After many repetitions of such behavior, the baby learns to leap into its mother's arms, at first, when a hand is extended to seize it, and later, at a mere gesture barely suggestive of the seizing movement. The mother frequently vocalizes when excited, the sounds accompanying her gestures. In the course of time, either the sounds or the gestures may serve as commands to the infant. These gestures or sounds vary from time to time under similar circumstances, and they seem to have no specific meanings that are recognized and responded to by the babies; instead, they are interpreted in connection with the environmental situation. Following a disturbance near their cage, the infant will be likely to respond to its moth-

er's call by rushing to her breast; but if everything in the environment is calm and serene, it will be more likely merely to change the nature of its activity. The infants also learn to express themselves. They extend their arms to their mothers to be picked up, they cry out in anger when their movements are hampered, and they shriek in fear when they discover themselves in precarious situations.

Among some adult chimpanzees, gestures with easily recognizable meanings develop. Some adults indicate negation by violently shaking their heads, and the desire for a companion to remain away from them, by pushing a hand outward from the body toward the other animal. They commonly indicate friendliness by extending the back of a wrist toward another animal, and they beg assistance by extending one hand or both hands, palms upward, toward an associate.

It has been indicated that communication in some form occurs between all social animals. There remains the question of whether subhuman animal forms possess a spoken language in which various sound patterns have specific symbolic significance.

Most birds in the wild stage have songs or calls that are characteristic of their particular species. That the songs are not inherited is indicated by the work of investigators, who have found that birds reared in captivity, away from others of their kind, develop songs of a nature quite different from that of the songs of their groups. Baltimore orioles isolated by Scott ⁽¹¹⁾ first developed call notes similar to those of wild birds of the same species, but they also developed distinctive songs which more nearly resembled those of the house wren. When six-day-old orioles were placed with adults which had been thus reared in isolation, they in turn developed and learned to sing the songs of their older associates. Conradi ⁽⁸⁾ reared young English sparrows in the same room with canaries. The sparrows first developed the characteristic chirp and then, later, learned to sing in

a manner similar to that of the canaries. When the sparrows were removed from the canaries, they lost their acquired song; but they soon regained it when they were returned to the original situation. Many birds, the parrot and mocking bird, for example, are known to imitate sounds they hear, though they usually retain characteristic call notes. It is apparent from evidence such as this that birds inherit a particular vocal apparatus and a tendency to use it—a conclusion similar to that drawn by Watson.^(15:142) The call notes characteristic of members of a species are the sounds naturally made with their particular vocal equipment. They are made with little or no practice and usually are retained in much their original form, regardless of environmental conditions. Many of the songs and imitative sounds, on the other hand, are acquired, and accordingly are more easily modified or lost.

The chimpanzee possesses vocal apparatus very similar to man's. Mrs. Learned,⁽²⁰⁾ who studied the vocalization of this animal, was able to distinguish thirty-two different sounds made by it. Various investigators have attempted to teach apes to speak. In most cases, the responses have consisted of mere twitching of the subjects' lips. In a few instances, these animals after prolonged training learned to say simple words like "cup" or "papa," though there was little evidence that they attached any specific meaning to the sounds. Several years ago, the author attempted to teach a female macaque to "speak" for food. When food was held before her, she extended her hands and by all manner of gesture and bodily position begged for it, but always without uttering a sound. Finally, another method was adopted. With the food in one hand, the experimenter played roughly with the animal until she became excited and shrieked. Each time she vocalized under these conditions, she was given the food. After repeated trials, she seemed to learn what was expected of her. When food was held before her and she was commanded to speak, she dis-

torted her lips and exhaled rapidly. After many weeks of training, she *learned* to make at command sounds similar to those which she was making daily when she was excited.

Though no extensive and at the same time satisfactory study of the speech of animals has yet been made, evidence such as we have just reviewed upholds the common opinion that the vocalization of animals occurs as an expression of their emotional state. There is some real question as to whether the majority of them are able to vocalize voluntarily without first learning to do so.

The conclusion to be drawn from our present knowledge is that no animals below the level of man have true speech. They do make sounds indicative of their emotional state. Vocalization of this nature, coupled with gesture and bodily movements and responded to according to the general environmental situation, serves as a means to intercommunication.

Summary

In this chapter, we have briefly surveyed various forms of social organization ranging from non-familial aggregations of relatively solitary organisms to complex communities composed of many families. We have seen how familial groupings are determined by reproductive functions and how they also are modified by physical environment and by structural, physiological, and psychological factors. Rather than an inherited tendency, gregariousness consists largely of habits of mutual adaptation that are formed by organisms reared in social groups and that are incongruous when the same organisms are isolated. Various forms of adaptive behavior, such as group play, coöperativeness, and communication, are essential to social life. These too, though limited and modified by the organism's structure, physiology, and physical environment, are largely adaptive habits

initiated during infancy and extended and perfected during the social life of the individual.

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CHAPTER XV

“Gifted” Animals

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Introduction

THE comparative psychologist frequently is confronted with the problem of analyzing and interpreting *unusual* animal behavior. He is told of and at times witnesses behavior of household pets or of highly trained animals that is far more complex than the usual activities of similar animals in the laboratory. Less often, a laboratory animal develops a strange new habit or responds in a puzzling manner under experimental conditions. Equally perplexing are the varying results that at times are secured by different experimenters when studying the same functions of similar animals. The purpose of this chapter is, first, to examine and interpret unusual behavior of animals; second, to point out factors that lead to it; and, third, to consider the significance of our findings when they are applied to laboratory investigations.

Examples of Unusual Behavior of Animals

The behavior of highly trained animals.—Frequently, the behavior of highly trained animals sets the lay public agog and challenges the wits of the psychologist in his efforts to explain it. In some instances, as in the case of Clever Hans and the Elberfeld horses, the behavior observed and the efforts of scientists to explain it aroused con-

siderable stir in both popular and scientific circles. Watson has brought together descriptions of the behavior of these and of several other "gifted" animals.⁽¹³⁾ We shall content ourselves with brief mention of these horses and then shall consider the unusual behavior of several other animals.

Clever Hans and the Elberfeld Horses.—Clever Hans was a stallion purchased by a Mr. Von Osten, of Berlin, in 1900, and later trained by the same man. When the horse was exhibited a little later, it had mastered a conventional alphabet and was able, so it appeared, to perform simple arithmetical problems. It could count all visible objects of a given class, such as hats or umbrellas, or could count the men or women present before it, differentiating the sexes. With its alphabet, it spelled out the names of objects presented before it. What is still more remarkable, it, like many human memory experts, carried the entire yearly calendar in its head.

After repeated demonstrations of these and other abilities, some of which were popularly attributed to occult power, Hans was made the subject of scientific investigation and report. Conclusions at first varied but finally Professor Stumpf, a psychologist, and his students, and Professor Pfungst, also a psychologist, determined that Hans could not solve problems nor correctly answer questions unless the answers were known to the questioners, and that the answers were determined by cues received from slight movements of the observers.

Von Osten died in 1909. Karl Krall, a citizen of Elberfeld who had worked with him, inherited Hans and in addition purchased other horses, which he trained. Muhamed, one of Krall's later acquisitions, was particularly adept at arithmetic. After two weeks' training of from an hour and a half to two hours daily, it could add and subtract digits and stamp out the answers with its forefeet. In three weeks, it was adding fractions, while after seven months' education, it could do sums involving square and

cube roots. Muhamed, according to Krall,⁽⁷⁾ mastered the concept of square root after this had been carefully explained and demonstrated to it during one lesson. The other horses behaved similarly, though less well in the use of the conventional alphabet.

Apparently, these horses had almost superhuman endowments, for few persons would be credited with learning a language in so short a time and then with utilizing it in comprehending arithmetical principles after a single brief lesson. But this was neither scientific proof nor disproof of their ability. Claparede,⁽¹⁾ when alone with the horses, presented them with cards bearing numbers that *he* did not know. Under these conditions, they made but from eight to thirteen per cent correct responses. Another observer noted that the animals started mechanically upon their answers without as much as looking at the letters and figures on the board before them. Hobhouse,⁽²⁾ in analyzing the results of the various investigations, found incongruities in the answers given by the animals. Thus, Muhamed failed to add $4 + 6$ and to multiply 6×6 in the same exhibition in which he solved $\sqrt[4]{2313441}$. In the case of another animal, it was found that in squaring numbers, results ending in odd digits were given, indicating a lack of familiarity with the principle involved. Though Krall, in describing the methods by which he trained his horses, indicated that he merely taught them how to express themselves by the use of their forefeet, one observer witnessed a performance in which the groom twitched the bridle at the moment when a blind stallion had stamped the right number. This use of the bridle in training the animals had not been mentioned by Krall. Its significance will be referred to later.

Though Krall may not have been guilty of conscious fraud, one is forced to credit him with exaggerated enthusiasms concerning the intelligence of his subjects.

Fellow, the performing dog.—The behavior of the dog

Fellow, though somewhat less spectacular than that of the horses we have just described, provides a more fruitful case for our consideration.

Fellow is a German shepherd male, one of many dogs bred and owned by a Mr. Jacob Herbert, of Detroit, Michigan. According to Herbert's statement to Warden and Warner, who studied the dog's behavior,⁽¹¹⁾ he tried to make the dog understand language in the sense of responding appropriately to commands. The dog was talked to a great deal almost from birth, in much the same manner in which a young child is spoken to during the years when it is developing speech. Scolding was the only punishment ever resorted to. According to the owner, the dog associates nearly 400 words with corresponding objects and situations.

When the dog was taken into the psychology laboratory to serve as a subject, the following precautions were observed: The owner made no attempt to use identical phrases in giving commands for a given performance. No set order was followed in the tasks the dog was called upon to perform. Commands were given in a conversational tone. Owner and investigators were concealed behind screens, where one of the latter observed the dog's behavior through a slit, while the other reported to the dog's master and indicated the commands to be given. Under these conditions, the dog responded readily and without error to over fifty commands such as "Sit down," "Stand up," "Roll over," and "Go and take a walk," in which the behavior did not involve definite identification of object or place, but consisted of movement of the dog's body. Acts requiring the dog to orient itself toward, and to identify, objects or particular places were performed with difficulty if the master was concealed from view. When Mr. Herbert, in full view of the dog, looked in one direction while commanding the dog to go to an object in the opposite direction, the animal followed the direction of the owner's gaze and was unable to carry out the command. When the dog was sent into a second room to

select one out of three objects which were placed out of his master's view, the responses were 53 per cent correct.

Particularly interesting in the behavior of this dog was the fact that it responded correctly when different words were used to express the same command and when similar words were involved in different commands.

Following these tests, according to Humphrey and Warner,* Mr. Herbert began training the dog to respond to commands given from behind a screen. The dog learned to depend far less upon his master's gestures, though it still was confused when gestures conflicted with spoken commands. Mr. Herbert's initial efforts were directed entirely toward teaching the dog to respond correctly to commands whether they were by word or mouth, or by gesture, or by both. The results indicate that the dog learned to respond to the combination of the two, depending largely upon oral cues for indication of the nature of the behavior and upon gesture for the locality or direction in which the behavior was to be enacted.

Dogs trained to work for their masters.—The World War gave great impetus to the utilization of dogs as servants to man. The recent increase in their use as guides for the blind and as police dogs has more fully demonstrated the degree to which they can be made to adapt their behavior to man's service. In a forthcoming book, Humphrey and Warner⁽³⁾ give a most enlightening description of the behavioral characteristics and capacities of these working dogs, of the methods whereby they are trained, and of projects through which they are being provided for such uses.

The sight of a thoroughly trained dog leading a blind man through the congested traffic of one of our city streets is enough to arouse doubt in some of us psychologists who are inclined to be extremely mechanistic in our views. At the end of a semirigid leash, the dog precedes its master in and

* See Chapter 9 of reference 3 in the bibliography.

out among pedestrians and under and around physical barriers. It is constantly on guard to protect its master from attack and it picks up any object that is dropped and communicates the fact of its recovery by pressing it against the leg of its owner. Commanded to turn to the right or to the left, it waits until a corner is reached and then obeys the order. At a crossing, the dog sits down at the curb and waits, not for a signal to go on, but until it sees its master's foot locate the curb. Then, when the traffic is clear, the dog proceeds across the street, changing its pace according to the demands of the immediate situation. Implicit and immediate obedience, according to the above authors, is one of the first and most important lessons learned by the dog. But in addition to that, it must learn intelligently to disobey. Thus, if it is commanded to advance into the path of an approaching automobile, it merely sits, and by its disobedience warns its master of the approaching danger. Here we have a situation where man is taught to respond to an animal. The dog is trained first, while the man who is to become its master must learn the meaning of slight changes of tension on the leash and of the dog's refusal to obey under given circumstances. Each must know when to, and when not to, respond to the other.

Police and patrol dogs are similarly trained for specialized duties in connection with the enforcement of the law. By their acute auditory and olfactory senses, they detect the nearby presence or approach of human beings of whom the officer frequently would be unaware, and give muttered warning of the fact. These dogs protect their master from attack, seize and hold suspects at command, and search out and retrieve objects thrown or dropped by suspects. For work along water fronts, they are trained to rescue drowning persons. Though gentle and obedient, they are ready instantly to leap at the weapon-bearing arm of an offender.

Complete description of the many services rendered by these working dogs cannot be given here. The facts that

accidents seldom occur to blind persons led by well-trained dogs and that officers once accustomed to the services of patrol dogs are averse to working without them indicate the degree to which these animals learn to meet the demands of their human masters.

Musical sea lions.—Yearly, in the circuses and on the vaudeville stage of this country, appear troupes of performing sea lions. These animals climb ladders and “walk” tight-ropes, and throw, catch, or balance balls with their noses even while balancing and propelling themselves on larger balls. Their remarkable sense of equilibrium, their lithe gracefulness, and, above all, the appearance of enthusiasm which they have while performing, make them especially popular as animal actors. Anyone who has observed sea lions at play in the wild state or in large aquaria realizes that much of their trained behavior represents adaptation and extension of their natural behavior for exhibition purposes. Without training, they frequently play about in the water, leaping, diving, and throwing and catching objects with remarkable skill.

The most significant demonstration given by some groups of these trained animals occurs when, at the command of their trainer, any one of three or four of them approaches a bank of horns and blows first sixteen and then twenty-five notes from *My Country 'Tis of Thee*. Their time is far from perfect, the proper length of notes is ignored, but the notes do occur in correct order and produce a recognizable tune. One animal appears eager to be through with his selections and to secure his piece of fish. Another plays more slowly. Though the trainer may stand several yards distant with his back toward the performing sea lions, if the animal plays a wrong note, it usually stops. This, according to their trainers, Messrs. John and Roland Tiebor, is their usual behavior. They believe that their sea lions have memorized both the order in which the horns are played and the resulting tune.

The ability to play at command and without direction not only one but two different and fairly complex musical selections, in addition to a varied repertoire of balancing acts, represents a degree of training seldom found in circus animals. Does it prove that sea lions are unusually intelligent? The answer is indicated by the methods used in training them. The horns are specially constructed with funnel-shaped ends. A sea lion is first taught to place his nose into one of the funnels and then exhale. This preliminary over, the animal begins learning the 16-note selection. It is made to play first this and then that horn in sequence until the selection has been gone through. Using this "whole" method of training, the performance is repeated time after time, day after day. Correct performances are rewarded, and punishment is used only to break bad habits. Though the sea lions soon learn the early lessons of their musicianship, three or four years' training may be required to make a satisfactory performer.

From the standpoint of the owners, sea lions are highly intelligent: they are exceedingly sensitive; they pay constant attention to their trainers during their performances; and, unlike many circus animals, they need not perform their various acts in the same order day after day. From a psychological standpoint, and when the methods of training are considered, it appears that these animals are both sensitive and highly adaptable, but that their behavior is more a reflection of the insight and patient perseverance of their trainers than of sea lion intelligence.

Unusual behavior of animals under controlled conditions.—Animals in the laboratory occasionally demonstrate behavior which, if unanalyzed, gives false impressions concerning their ability to respond to supposedly controlled cues.

Johnson,⁽⁵⁾ while studying visual pattern discrimination in the dog, monkey, and chick, set up an experimental situation in which the subjects, upon exposure of appropriate

visual stimuli, were rewarded if they entered the proper alley but walked onto a charged electric grid if they chose incorrectly. The dog subject appeared to detect finer differences in the stimuli than the investigator expected. But before responding, the dog usually sniffed at the electric grids. When the experimental situation was changed so that the grid in the “wrong” alley was not charged until the dog was upon it, the animal’s proficiency was greatly reduced. The dog’s early responses had been determined olfactorily by the presence of ozone or of other chemical differences in the charged field.

In connection with a study of brightness discrimination in dogs following removal of the striate cortex, Dr. D. G. Marquis first trained subjects to wait at a certain point in an alleyway and then to proceed forward to receive food when an electric bulb was illuminated.⁽⁸⁾ After the removal of the striate cortex, the subjects responded in the same manner. Here was evidence that, while not in serious conflict with the investigator’s later findings, was not satisfactory to him. When he substituted a blackened light bulb from which no light was emitted, the dogs continued to respond correctly whenever the electric circuit was closed. Study of the situation proved that the dogs had learned to respond to a slight sound made by the filament of the bulb whenever the current was turned on.

To these two cases in which laboratory animals were concerned, we may add that of the author’s dog, which without training learned to open an office door. The dog, a large animal, surprised its owner by suddenly opening the door to the latter’s office and entering. The animal was placed out of doors, but soon reentered in the same manner. The dog was again ejected, but this time the owner concealed himself where he could see how the animal manipulated the latch. The dog went to the door and placed his muzzle against the keyhole, apparently better to determine by smell and hearing what was going on inside. Soon the dog’s

muzzle dropped until it rested upon the latch button. When the pressure became great enough, the latch was depressed and the door opened. Time after time, this was repeated by the dog until it finally learned to go to the door, place its muzzle upon the latch, and then enter. Here was intelligence to the extent that the dog had associated chance behavior with the process of opening the door, but it was not the degree of intelligence that might have been attributed to the pet if the conditions under which the habit was formed had not been known. Though such behavior is not complex, when either the laboratory animal or the household pet develops several responses of this type without tuition, the performance may suggest a degree of intelligence that is entirely out of keeping with the facts of the case.

Animals reared in a human environment.—In 1914, Watson ⁽¹³⁾ concluded a chapter on the limits of training in animals by pointing out that upbringing in the home, where the subjects are in constant contact with human beings, produces in them a complex type of behavior that our present laboratory concepts are inadequate to explain. He further suggested the need of a station where the chimpanzee could be bred and where the newly-born chimpanzee and the newly-born child could be brought up side by side and subjected to the same training.

The need so well stated by him was in part realized in 1932 when Dr. and Mrs. W. N. Kellogg borrowed a seven-and-one-half-months-old female chimpanzee from the Anthropoid Experiment Station of Yale University in Florida and for a period of nine months reared it with their ten-months-old son.⁽⁶⁾ Child and chimpanzee were kept under as nearly identical conditions as was possible, and their physical and behavioral development were carefully studied. Clothes, food, and playthings were as similar as possible for each of them. The same habits of sleeping, of eating, and of hygiene were encouraged in both subjects. These

two babies, human and ape, were taught no tricks, though they were given every encouragement toward behavioral progress.

Within a few weeks after the experiment had begun, the child and the ape were happy companions in the same household. Both were as well-behaved as most children are, whether they were eating in their high-chairs, being placed in their respective beds, or greeting visitors by extending a hand to be shaken.

At the beginning of the experiment, the ape, Gua, though younger, was further developed physically than the child, Donald—a matter in keeping with the fact that chimpanzees reach sexual maturity three or four years earlier than human beings. This physical disparity between the two increased throughout the time of the experiment and was accompanied by an increasing relative proficiency on Gua's part in motor performance tests that are appropriate for children of that age. These results must not be interpreted as indicating that the young ape was more intelligent than the child. Instead, the ape was approaching the limits of its behavioral capacity more rapidly than the child.

Particularly important to us here is the nature of Gua's adaptation to her human social environment. Stimulating to and in turn stimulated by the child, the ape not only did most of the things young apes do, but in addition did many things that children do. She soon adapted herself to wearing clothes and to the use of dishes and the various conveniences of the home. Automobile rides, particularly with opportunities to honk the horn or jingle the car keys, were one of her greatest sources of pleasure. She and the boy joined in childish games. With only a little encouragement, she frequently rose from the quadrupedal form of locomotion most common to chimpanzees and walked upright for long distances at a time. Socially, she was more dependent upon her master than Donald was upon his mother.

When the investigation was ended, Gua was removed from her companion Donald and from the adults in whose constant care she had been for nine months. Without clothing and separated from human household environment, she was placed in an ordinary cage with few opportunities for activities such as those to which she had become accustomed. For several hours each day, she served as an experimental subject or otherwise had human associations. But now, with the habits of a child, she was in the environment of a chimpanzee. Her adaptation to the transition was slow and was accompanied by much emotional disturbance. Within a few months, however, her behavior generally was undistinguishable from that of the ordinary laboratory chimpanzee.

Though this investigation involved but one animal and unfortunately could not be continued over a longer period of time, the results are particularly significant here because the behavior of the chimpanzee Gua can be compared with that of several other chimpanzees that have been reared under various conditions of domestication and of formal training. Nissen ⁽¹⁰⁾ reports that chimpanzees that have not been domesticated do not manifest the complicated behavior mechanisms characteristic of those in captivity. This is true because their material requirements are simple and are easily met in their field environment, and we should add, because stimulation from their environment is less great. Two baby chimpanzees which the author observed while they were being reared with their mothers demonstrated little of the complex behavior described for Gua. They learned to eat and to climb about their cages, and they engaged in simple play activities with their mothers. Their interests during their first year began to be directed toward the locks of their cages or to the faucets from which the older animals secured water. But these baby chimpanzees had but the maternal companion and the environment provided by their cages. Furthermore, their ma-

ternal tuition, as described in Chapter XIV, was largely carried on by the process of inhibition rather than that of stimulation. Their behavior was typical of that of the caged chimpanzee and was little if at all more complex than that of chimpanzees in the field.

The chimpanzee Alpha, who was separated from her mother at birth, was studied during her first year by Doctor Jacobsen and Doctor Yoshioka.⁽⁴⁾ Largely as a matter of expedience, she was kept at the Jacobsen home much of the time. Unlike Gua, she was kept merely as a subject for the study of growth and of unencouraged behavioral development. Although her position in the home was like that of the ordinary household pet, her environment in most respects was far more varied than that of chimpanzee babies reared by caged mothers. She soon learned to use cups and spoons; doors were objects to be opened and closed; she responded to many commands; her dependence was centered upon her human caretakers. Though in the resemblance of her behavior to that of a child she took an intermediate position between Gua and the mother-reared babies, in such portions of normative behavior tests as were applicable to her, she demonstrated potential abilities similar to those shown by Gua. Except for the presence of Gua's child companion, the physical environments of Gua and Alpha were similar. This fact lends force to the assumption made by the Kelloggs that in Gua's behavioral development the *psychological* environment was the important factor.

In contrast to chimpanzees whose behavioral development has occurred largely through their adaptation to human environment are those animals which have been trained as vaudeville performers. Notable among these was the chimpanzee Peter, who appeared on the vaudeville stages of this country some twenty years ago. On the stage, he skated, rode a bicycle, lighted and smoked cigarettes, and while sitting at a table, ate with knife and fork and drank

from a bottle. When taken into a psychological laboratory, ⁽¹⁴⁾ he strung beads, unlocked padlocks with a key, used hammer and screwdriver appropriately, and did at command many other things that made a profound impression upon his observers. Peter was a performing animal in which advantage had been taken of chimpanzee ability to duplicate many of the motor activities performed by man. Though he was able to do the things described, his behavior largely was initiated by the commands of his trainer, and there is little evidence that he either understood or secured satisfaction from the acts themselves.

The dog Fellow, which we described above, responded to long training and to long association with human beings by learning to respond to many more commands than are recognized by most dogs. In the particular direction in which it was educated, namely, that of responding to commands, its behavior probably represents the maximum achievement so far made in dog training. The chimpanzee Gua, with neuromuscular equipment more nearly resembling man's, became more fully adapted to human environment. Without the same degree of formal training, this animal developed habits of doing things voluntarily that were comparable in complexity with the acts performed by the trained chimpanzee Peter, in response to command.

The behavior of these animals might be interpreted as indicating that they were much more intelligent than others of their kind. But does the evidence justify such an interpretation? The dog Fellow probably was more adaptable than the other dogs owned by Mr. Herbert. Gua and Alpha may have been superior to the average laboratory chimpanzee, though their observers found no evidence to that effect. On the other hand, when the individual acts of these animals are considered separately, one finds that they do not represent behavior at a higher level than is typical of other similar animals. The only conclusion we can draw is that they responded appropriately to an unusual variety of situations

which resulted from the varied physical and psychological aspects of the human environment in which they were reared.

Factors Involved in Animal Training

Before we can interpret the behavior of trained animals, we must examine some of the factors involved in their training. The animal trainer is not interested in *how*, *why*, or *under what conditions* his subjects learn to make their responses, but rather his interest lies in getting them *to perform*.

The trainer first decides what he wishes his animal subjects to do, and then arises the problem of causing the animal to do it. If the subject is dangerous or powerful, it may be driven, through fear of punishment, to act in the desired manner. Thus, an African lion was trained to draw a chariot by being driven before pistol and whip to a position where the yoke attached to the chariot shafts fell over its neck. By many repetitions, after each of which it was rewarded with food, it learned to take its position before the chariot and permit the yoke to be lowered into place. An animal may be enticed to act as desired if food is so placed that the animal can secure it only when he behaves appropriately; for example, a trainer succeeded in getting a dog to walk on its hind legs by holding food just out of reach above it. Again, one may cause an animal to perform the act by forcing it into the position desired; for example, a horse learns to kneel when its knees are bent under it either by hand or by the use of ropes. Another method which is commonly used is that of causing an animal to do something which it does readily and then gradually changing the situation until the animal does the same act under what originally would have been difficult circumstances. In this manner, one can teach an elephant or a horse to mount a relatively small pedestal by leading it first onto large platforms and then onto smaller and smaller

ones until the desired size is reached. By similar methods, either of these animals may be taught to walk on narrow planks much as human performers walk the tight-wire. By a somewhat similar method, an animal is first taught to make easily elicited responses in a simple situation, and then the situation is gradually changed or complicated until the animal has to alter and extend its behavior to accomplish the same end result. Humphrey and Warner describe the use of this method in teaching dogs to retrieve.⁽³⁾ Most dogs, as a form of play, learn to carry objects or to chase objects which their masters throw. When being trained, the dogs are first taught to retrieve at command thrown objects and to give them to their trainer. Then, the objects are thrown when the dogs are not present. At the command to fetch them, the dogs start, but not having seen the objects thrown, they use their noses to locate them. By appropriate variation or increase of the time interval, of the number of objects thrown, or of the individuals who throw them, the dogs finally learn to locate and to retrieve objects thrown or placed by human beings other than their masters. By similar methods, the dogs may be taught first to retrieve objects thrown into water and later to rescue drowning persons.

Though methods of initiating various types of behavior vary according to the trainer, the subject, and the behavior itself, some combination or modification of the methods of force (putting the animal through the act), enticement, and adaptation of natural or easily elicited behavior is generally used.

The cues to which trained animals respond.—When an act is initially performed by an animal, all features in the environmental situation constitute potential elements for the cue-situation which is to be built up. Physical surroundings, time of day, events that have preceded, the presence of objects of fear or food, and the behavior of the trainer are but a few of the many factors that may become

associated with the act. As the act is repeated time after time, certain of these features become associated with the behavior as initiating or controlling cues. The oral command of the trainer frequently is accompanied by gesture. The gesture may develop from movements made by the trainer in forcing the animal to go through the act, such as a circular movement of the hand when commanding a dog to roll over. Again, the trainer may indicate by changes of posture or by movements of his hands when the animal shall begin or stop behaving as it has been directed. After the act is performed, the animal is usually rewarded with food or spoken praise or both, and its behavior then becomes anticipatory in nature.

Frequently, as might be expected, the cue-situation includes various factors of which the trainer may or may not be aware. Some circus animals will perform their acts only in a definite sequence, and some will not perform outside of the circus ring. A good example of the inclusion of environmental factors in the cue-situation occurred in the case of a monkey which the author trained to somersault by "putting it through" the act. The little animal learned the trick after a very few trials, and then an effort was made to have it demonstrate the behavior before a class of students. It was brought from its quarters-room to the classroom, where, when placed first on a table and then on the floor, it was commanded to "somersault." Each time the command was given, the monkey looked up at its master and nervously smacked its lips, but did nothing more. Finally, it was led into the hall of the building, where the command was given once more. Here without hesitation the monkey somersaulted. Investigation showed that one of the features causing its previous failure was the fact that in the quarters-room and in the hall there were linoleum-covered floors, while the classroom floor was carpeted. The animal had learned to somersault in response to gesture and

oral command, and when on linoleum. Further training was required before it would perform otherwise.

As an animal subject progresses in its training, various features of the original cue-situation may become disassociated. A seven-year-old horse belonging to the author was trained to tell its age by pawing with one forefoot. In the initial situation, the command was given, the horse's head was held down by the bridle rein, and it was forced to paw until its head was released. Later, it was necessary only to give the command and hold the animal's head down. Finally, it would begin pawing at command and would cease at any time after four or five strokes if the trainer or an observer either turned away or made the slightest movement of the "bridle" hand. Under these conditions, an observer, knowing the age of the animal, ordinarily would unintentionally give it the cue to stop pawing when the seventh stroke was reached.

The complexity of the original cue-situation has been demonstrated not only in cases such as these, but also in a number of laboratory experiments where it has been found either that animal subjects were not responding to the primary cue provided in the experimental situation, or that they were responding to a combination of this and other cues.

The complexity of motivation.—Just as the cue-situation to which trained animals respond is both complex and variable, so also, though perhaps to a lesser extent, is the nature of their motivation. The problem of motivation as studied in the laboratory has been discussed in Chapter IV. For our purposes here, we shall only point out that though hunger for food and fear of punishment are the commonest forms of motivation used in training animals, many other less objective factors are involved. Praise or criticism from the trainer frequently is more effective with a highly adapted animal than other forms of reward or punishment. Some animals seemingly derive pleasure from performing

their learned behavior, and there are fairly well authenticated cases where such behavior has been continued by them in their quarters away from their trainer and the usual cue-situation.

Other factors involved in animal training.—When a rat is initially placed in a maze, it runs wildly about, exploring the side-walls, floors, and ceiling, and devoting little attention to the maze-path or maze-pattern as such. After locating the food once or twice, its behavior quite suddenly changes, and it seems to set about the task of seeking it. If the same rat is run through several mazes, it becomes “maze-wise,” and much of its early exploratory behavior drops out. Then any maze almost immediately arouses its food-seeking responses. In a similar manner, monkeys and chimpanzees that have long been used in behavioral experiments arrive at a stage at which, when taken into an experiment room, they at once begin examining and manipulating any apparatus present, as if looking for a to-be-solved problem. Performing animals show similar cumulative effects of training. Once taught to respond to two or three different commands, they learn to attend to their master’s voice or to his gestures, or both, as the case may be. In the same manner, negative or positive transfer occurs. Thus, an animal already taught to lie down at command is easily trained to roll over, but an animal that has learned to roll over may have difficulty in learning to somersault.

Another important factor is the rapport which is built up between the animal and his master. Animals, like children, are friendly to some people, avoid others, and learn to obey the commands of some and disregard those of others. To the performing animal long in the hands of a trainer who demands obedience and at the same time commands the “affection” of his subjects, a word of praise or of criticism frequently is more effective than more material forms of reward or punishment. The animals form habits of adapting their behavior to the desires of their masters.

Interpretation of the Behavior of Trained Animals

At times, our discussion has wandered afield from the actual behavior of animals and its interpretation. We have considered unusual behavior of both trained and untrained animals, and factors involved in the acquisition of such behavior. We now turn to the problem of the interpretation of this behavior.

Another important factor is the adjustment of animals to both their masters and their environment. Jackson ^(3a) in a splendidly conducted study of transfer of training in albino rats found that in a given maze the learning of his subjects was facilitated during their first five or six trials if previously they had opportunity to adjust themselves to the laboratory, if they were handled daily by the experimenter, if they were trained in other types of apparatus, or if they were run through other mazes. The feature of his results which is significant to us here is the fact that handling alone was practically as effective as experience in other mazes. When animals are worked with frequently, there arises a definite rapport between them and their master.

Highly trained animals whose behavior has been reported have frequently been selected for their adaptability. Von Osten owned but one Clever Hans, though his successor, Krall, trained several stallions to perform in comparable manner if not always with equal proficiency. The dog Fellow probably was more adaptable than most dogs. Many animals prove themselves unfit as circus performers just as many rats are unsuitable maze subjects. Dogs which are to be trained for police purposes or to lead the blind are not only selected, but now are being bred selectively for those factors which make them best suited for such work. From this it appears that animals chosen for intensive training are usually highly adaptable. This,

however, means, not that the individuals selected are animal geniuses, but rather that stupid animals are usually eliminated.

So far, we possess little knowledge concerning the relation between trainability and intelligence. There is some evidence that among human beings, individuals of low intelligence learn to perform routine acts more readily than do their more intelligent fellows. Rats at times respond more readily than do monkeys in situations requiring no insight or comprehension of the problem. From this fact, it seems that ability to perform routine acts such as characterize the performances of many circus animals is a poor indicator of intelligence. High in the scale of this type of performance is the varied behavioral repertoire of the musical sea lions we have described. The ability of the Elberfeld horses to stop pawing when correct answers were reached indicates little more than sufficient sensory acuity to respond to minimal cues, though some of their responses of a more obvious and less spectacular nature better demonstrate the degree to which they had learned to respond to various forms of command.

In most instances where so-called “gifted” animals have been exploited by their owners, reliable information concerning the exact methods and the extent of training has not been available. Thus, Krall’s failure to mention the use of the bridle in the training of his horses probably resulted in obscuring the nature of the cues to which his animals responded. As we saw in the case of the horse that learned to tell its age, the use of the bridle paved the way for this animal to learn to respond to minimal postural changes on the part of the observer. Though we cannot detail the exact methods of training used in all of the cases cited, the principles of training are sufficiently well-known to enable us within limits to interpret the results. In the first place, a definite rapport between trainer and animal is established in which the latter, stimulated by rewards or

inhibited by punishment, learns to adapt its behavior to its master's desires. The animal forms habits of attending to cues and develops facility in associating these cues with given acts. There then follows a period of training during which the subject usually learns to perform a great variety of acts in response to openly given cues, as in the case of the dog Fellow, or in which it performs a few relatively simple acts that are initiated by obvious cues and are concluded in response to minimal cues from the experimenter, as was the case with the Elberfeld horses.

When the problem is approached in this manner, it appears that most highly trained animals have been fairly ordinary individuals. Their training has been more unusual than their ability to respond to it.

Interpretation of the Behavior of Laboratory Animals

It is not uncommon for different experimenters to secure highly different results when using similar animals in supposedly similar experimental situations. Such diversity of findings often arises from the failure of the experimenters to recognize and control factors such as we have been discussing. The age and past experience of the subject; the nature of the experimental set-up and of the cues included in it for the animal to respond to; the manner in which bait and punishment are used; the frequency and order of trials—all of these fairly obvious and fairly objective factors must be known for correct interpretation of the results. But they are not the only features of the experimental situation that must be considered.

The relationship between animal subject and experimenter and the manner in which the subject is handled are important. One investigator seizes his rats and dumps them into the maze as dispassionately as if they were mechanical robots. Another fondles and pets his rats until, though hungry, they loiter in the starting chamber to be

near him. Others, still worse, vacillate between such extremes according to their moods. With highly adaptable animals, such as dogs, monkeys, or apes, demonstration of praise or criticism by the experimenter may be a more potent reward or deterrent than food on the one hand or electric shock on the other. In investigations concerning *how* animals behave, this subject-experimenter relationship is not so important; but in studies of animal capacity, comparable results will not be secured by various investigators until comparable animal-handling techniques are used. In matters of animal motivation and of techniques in handling animal subjects, the psychologist has much to learn from the professional animal trainer.

We mentioned two experiments, and many others could be added, in which animal subjects were found to be responding to other cues than those intentionally included in the experimental set-up. As we saw in the case of trained animals, everything in the environmental situation is a potential cue. Sequence of events, behavior of the experimenter, and sounds or movements of parts of the apparatus all or partly may enter into the cue-situation. To determine to what degree any of these are involved necessitates careful controls and tests of the subject's responses. It is not sufficient, in many studies, merely to determine that the subject's responses break down in the absence of the experimentally provided cue, for this cue may be but a part of a larger cue-complex to which the subject is reacting. Experiments are frequently mechanized in an attempt to control the cue-situation, particularly cues from the experimenter. But apparatus in which the experimenter can see or hear the subject is usually apparatus from which the subject can likewise see or hear the experimenter. Regardless of the nature of the experimental set-up, tests should be made for cues both from the experimenter and from the experimental set-up.

Knowing the conditions under which the experimental

data have been secured, what precautions must be taken in interpreting them?

At the time of the reaction to the anthropomorphism of the anecdotal school of animal psychology (see Chapter II), Lloyd Morgan formulated the following principle, since known as "Morgan's Canon":

In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale. (9:53)

The various conscientious efforts to apply this principle, though in general beneficial to psychology, at times have been questionable. Within recent years, experimenters have devised problems the solution of which required previously defined and named behavioral processes. When it was found that subhuman primates solved these problems, the experimenters, apparently to avoid appearances of anthropomorphism, redefined and renamed the behavior demonstrated by the animals. To thus brand the same form of behavior one thing when it occurs in monkey and another when it occurs in man, is comparable to differentiating between the "sweating" of monkey and the "perspiring" of man.

Other investigators, for similar reasons, have avoided stating their honest convictions concerning the behavior they have observed. The purposes of science demand accurate observation, accurate description, and, where possible, logical interpretation. Though all interpretation is subject to modification or even to reversal, no one is in as good a position initially to evaluate the various factors that enter into an investigation, and to interpret the results, as is the collector of the data. The anthropomorphic phobia has no place in scientific psychology.

We have seen how Clever Hans and the Elberfeld horses behaved in a manner which gave them the appearance of

possessing superhorse endowments. Analysis of their behavior, however, proved that the explanation of it lay in their ability to respond to minimal cues from human observers. The dog Fellow greatly excelled the average dog in the number of commands to which he could respond correctly. But practically all of his responses, when considered individually, fall within the known behavioral limits of well-adapted canines. The behavior of animals is determined and limited by their anatomical and physiological equipment and is modified by their environment and past experience. With these facts as a basis, various attempts have been made to establish behavioral or structural criteria from which the presence of “mind” in organisms could be inferred. But such efforts have been largely fruitless. As Washburn has said, “There is no such thing as an objective proof of the absence of mind.”^(12:25) So far as we now know, man, monkey, and rat are all capable of the same behavioral processes, though these are differently manifested and appear in widely varying degrees. We can, however, expect greater similarity in these processes between animals in which there is greater similarity of structural and functional equipment. This being the case, when we observe in an animal behavior that greatly transcends in complexity that which under the same or similar conditions is typical of other animals of the same species, we must look to the conditions of our experiment for the answer. If we do not find it there, judgment must be withheld until similar behavior is observed under other circumstances.

Conclusions

When the behavior of so-called “gifted” animals, which frequently seems more complex than that observed in the laboratory, is analyzed with regard to its origin, it appears relatively commonplace. Household pets, in the course of

adapting themselves to their human environment, develop many new forms of response without tuition. When the psychological aspect of their human environment is enriched, they adapt their behavior in more numerous ways, and it is the number rather than the nature of their responses which makes their behavior appear unusual. The acquisition of behavior by highly trained animals is facilitated by such factors as the rapport between trainer and subject, the methods whereby the animal is handled, negative and positive transfer, and highly complex motivation. Frequently the selection of commands or cues which are obscure to the observer gives a false impression of the nature of the subject's responses.

The original cue-situation that an animal learns to associate with given responses may include many factors in the environment. As training progresses, the less constant of these are dissociated. The trainer, intentionally or otherwise, may cause his subject to dissociate all obvious cues and to respond to obscure bodily movements of his own or of observers. After such training, animals such as the Elberfeld horses appear to be able to answer questions or to solve problems when in reality the answers are being provided by the trainer or observer. The complexity of the initial cue-situation and behavior of the type just mentioned are particularly important to the psychologist because laboratory animals occasionally learn to respond to factors not intentionally included in the experimental set-up, such as movements of parts of the apparatus or of the experimenter.

The relationship between experimenter and subject and the method of handling subjects are too often ignored by psychologists. They frequently are responsible for the divergent results secured by different experimenters when using similar animal subjects.

Though great caution is necessary in the interpretation of animal behavior, Morgan's Canon has led to an an-

thropomorphic phobia that has no place in scientific psychology. The discovery of a type of behavior in animal that is present in man seldom justifies redefining and renaming the behavior of the animal on the *a priori* basis that animals are incapable of behavior at such a level. When, however, animals appear to demonstrate more complex behavior than that which is typical of their kind, the method of its acquisition should be examined. If an explanation of its difference is not found as a result, judgment should be deferred until comparable behavior is observed in similar animals under other conditions.

There still is much to learn concerning the complex behavior of highly trained animals. Our present knowledge indicates that it is their training rather than any unique individual talent that must command our attention.

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